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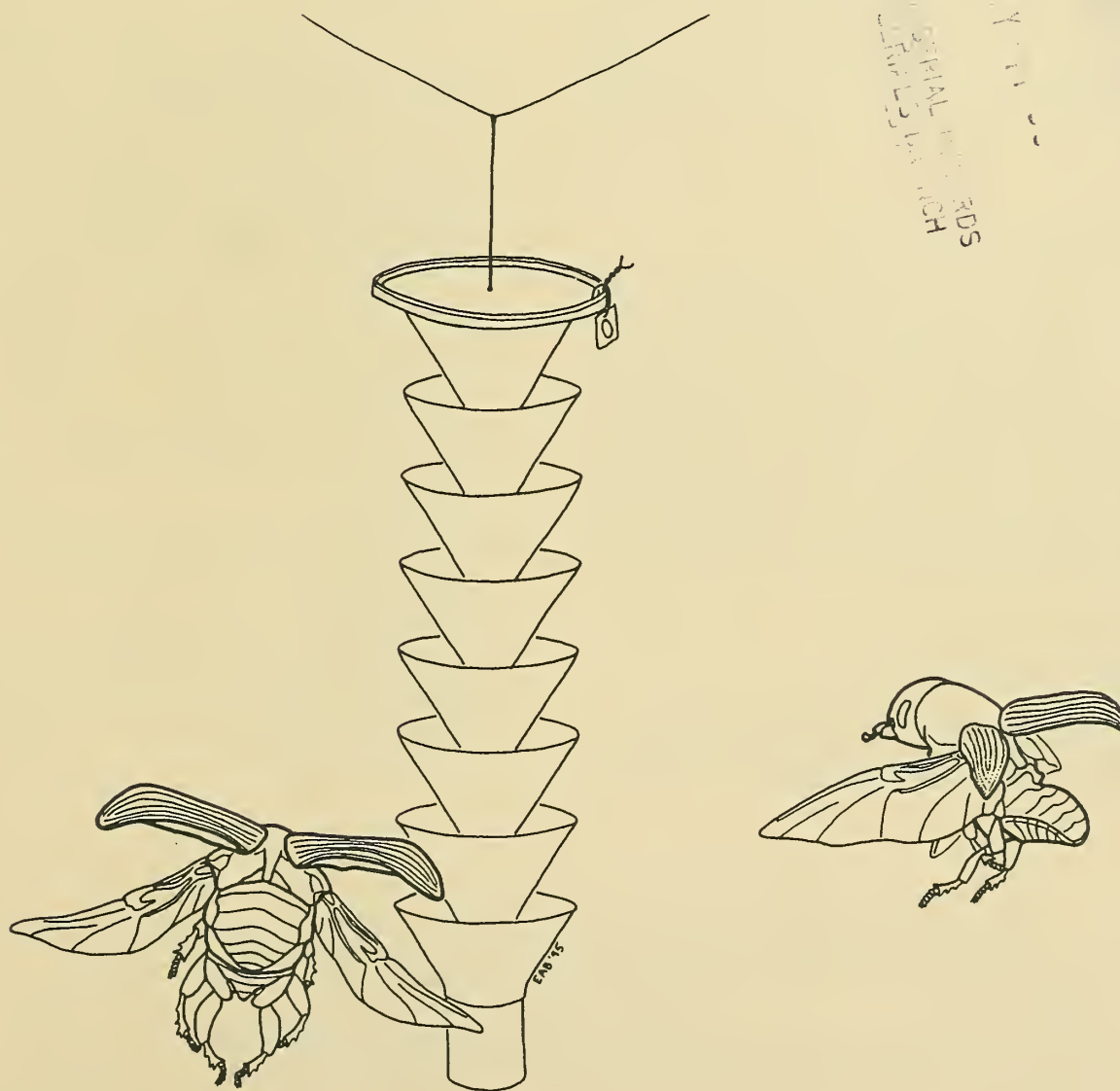United States
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Application of Semiochemicals for Management of Bark Beetle Infestations—Proceedings of an Informal Conference

The Technical Editors

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Research Summary

This report includes 10 papers presented at an Informal Conference entitled "Application of Semiochemicals for the Management of Bark Beetle Infestations," held at the 40th national meeting of the Entomological Society of America. Indianapolis, IN. December 12-16, 1993. These papers present the latest information on the status of semiochemical-based pest management research and application for the major bark beetle species impacting North American coniferous forests.

Acknowledgment

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Annual Meeting of the
Entomological Society
of America

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Introductory Remarks: Informal Conference on Application of Semiochemicals for Management of Bark Beetle Infestations

Scott M. Salom
Kenneth R. Hobson

Researchers today are tantalizingly close to developing semiochemical-based tactics for operational use in the management of several bark beetle species. This is exciting, especially for those involved in research and development of these economically viable and environmentally benign tactics for the last three decades. For some bark beetle species, research is only beginning, or continued research is clearly needed. However, for a few species the technologies and protocols are basically in place and may need only minor modifications or refinements before they are ready to be integrated with pest management practices.

Once the techniques are ready for operational use, it is imperative that we successfully transfer this technology to forest managers, technicians, and other potential users. The successful implementation and integration of these tactics with other suppression strategies are dependent, in part, on the time and effort put into developing effective educational programs and support to all users. Misuse or misapplication of the new techniques could lead to failures, resulting in loss of confidence by users, and setting back their implementation.

As semiochemical-based pest management tactics begin to be used for surveying, suppressing, and manipulating bark beetle populations, we felt it would be a good time to convene with experts familiar with some of the major bark beetle pests. Presentations focused on the history of this effort, on the status and future of semiochemical-based tactics for some of the more important bark beetle species, on the future directions of research, and finally, on transferring technology to land managers and other potential users. Many of us will be faced with considering this last area soon. The conference program met our objectives well and we were pleased with the willingness of the participants to contribute to this effort.

An important and insightful overview of semiochemical research is provided by John Borden who discusses the development of methodology used to isolate, identify, and characterize the role of behavioral compounds produced by bark beetle species and their host trees for communication, colonization, and proliferation of infestations. The discovery of pheromones and host volatile synergists or attractants promised revolutionary advances in the way pest managers would be able to confront bark beetle outbreaks. We realize that development of pest management strategies that utilized these advances presented a whole new set of challenges to the researcher. Although we see a sobering view of the trials and tribulations of investigators, success stories are beginning to appear and a bright future for semiochemical-based pest management of bark beetle species can be counted on.

Research efforts for the most important North American bark beetle species are at different stages of advancement and development. Ronald Billings and others describe the development and use of southern pine beetle (*Dendroctonus frontalis* Zimmerman) semiochemicals for different pest management objectives that include using inhibitors for suppression of infestations, using inhibitors and attractants for manipulating direction of infestation growth, and using attractants for monitoring populations and forecasting their trends on a regional basis.

Research efforts for bark beetle species of western North America are perhaps furthest along for the mountain pine beetle (*Dendroctonus ponderosae* Hopkins).

Gene Amman and Staffan Lindgren describe use of attractive baits for management tactics including detection, containment and concentration, logging mop-up, and spot suppression. Antiaggregation pheromones initially produced promising results, but later ambiguous results revealed a number of potential problems and the need for additional research.

Richard Werner and Edward Holsten describe the objectives and subsequent efforts of Forest Service research, development, and application using semiochemicals to manage spruce beetle (*Dendroctonus rufipennis* [Kirby]) in Alaska. Research on semiochemical-based pest management of the western pine beetle (*Dendroctonus brevicomis* LeConte) is being revived with efforts by Timothy Paine and S. L. Bertram, who have been studying the potential for using semiochemicals to protect high value trees. A case study of a disastrous bark beetle outbreak at Torrey Pines State Reserve is presented by Patrick Shea and Michael Neustein; they successfully used semiochemicals to suppress an outbreak of *Ips paraconfusus* Lanier and thus prevent the destruction of a rare natural stand of *Pinus torreyana* Parry ex. Carr.

The study of host compounds has not received as much attention by researchers as have compounds produced by insects. Kenneth Hobson explores the opportunities and potential for this avenue of research.

Gerhard Gries looks at the prospects for continued study of bark beetle semiochemicals and associated new technologies. The new advances he describes will lead to the improvement of the standard protocol of isolation, identification, and biological characterization of semio-chemicals that has been used for the past three decades.

All the efforts described in the following pages will be fruitless unless we are able to transfer this technology to land managers. James Johnson describes the conceptual basis of technology transfer. He provides detailed recommendations for ensuring success at the operational level. Anything short of a complete and effective educational transfer to forest managers and other targeted users would be unacceptable. Successful technology transfer will ensure that all the efforts made by past, present, and future researchers will not be wasted.

From Identifying Semiochemicals to Developing a Suppression Tactic: a Historical Review

John H. Borden

Abstract—Although European foresters in centuries past unknowingly used semiochemicals in employing trap trees against bark beetles, it was not until the last half of this century that research disclosed the semiochemical-based nature of the biology of bark beetles. The isolation, identification, synthesis, and bioassay of bark beetle semiochemicals have traditionally followed a standard protocol developed in 1967 by R. M. Silverstein and his co-workers. With only a few modifications, application of this protocol has resulted in the discovery in bark beetles of six new types of semiochemicals. Knowledge of bark beetle semiochemicals has led to fundamental contributions to chemical ecology. Although early research showed great promise for the practical development of semiochemicals, development has been confounded by inadequate evaluation and lack of comprehension of the complexity of the natural systems involving semiochemicals. Nonetheless, a number of semiochemical-based tactics are ready for use.

When a European forester in centuries past felled trap trees for bark beetles (Coleoptera: Scolytidae), he was unknowingly using a semiochemical-based suppression tactic. He started the tactic by killing the tree. The ensuing release of volatiles from the felled tree, and the first-attacking beetles, resulted in a semiochemical-mediated mass attack. Large numbers of beetles were then absorbed in the felled trees, diverting them from standing timber.

In the latter half of this century, researchers have discovered, for some species of bark beetles, why mass attack occurs, and what specific semiochemicals are responsible for controlling them.

Because of research success, we have been able to devise innovative ways in which semiochemicals can be used to improve on the trap tree methods of the past. With reference to research in the past three decades, my objective is to review the process by which semiochemicals for bark beetles are identified, characterized, and developed for use in forest pest management programs.

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Isolation and Identification of New Semiochemicals

The discovery of new semiochemicals for bark beetles has demanded a strange wedding between dirt forest entomology and state-of-the-art organic chemistry. In some rare cases, "gynandromorphs" have occurred that embrace both disciplines in the same individual. A standard protocol for isolation and identification of new semiochemicals was clearly elucidated by Silverstein and others (1967). Although there are now modifications and shortcuts for this protocol, it remains the fundamental basis for the discovery process.

There are six elements to this protocol: (1) development of a laboratory bioassay; (2) production of large amounts of starting material; (3) isolation of active components by separatory methodology, monitored at each step by bioassays; (4) identification of individual active components by spectrometric techniques; (5) confirmation of postulated structures by comparison with rationally-synthesized compounds; and (6) confirmation of biological activity of synthesized compounds by laboratory and field bioassays. This protocol was developed while Silverstein and others (1966) were engaged in the first successful isolation and identification of bark beetle aggregation pheromones, for the California fivespined ips (*Ips paraconfusus* Lanier). It is impossible to go wrong if one sticks to this protocol, but it can be difficult to follow if beetles in a given species are uncooperative in bioassays, or if pheromones are present in minute quantities. Therefore, researchers have developed various technological improvements since 1967 that have made the process easier.

Treatments with juvenile hormone analogues have been proposed (Gerken and Hughes 1976) and used (Francke and others 1977) to enhance the pheromone content in beetles from which the starting material is extracted. Such treatments are particularly important if it is difficult to collect or produce large numbers of beetles, or if they produce very little pheromone per individual. They can pinpoint potential pheromones because hormone-enhanced materials may increase in proportion to others. In conjunction with "differential diagnosis" of sex-specific volatiles (Vité and Renwick 1970), hormone enhancement can be a very powerful tool.

The innovations of capturing volatiles in Porapak Q (Rudinsky and others 1973; Byrne and others 1975), or cryogenic traps (Browne and others 1974), eliminated from contention many compounds previously extracted from frass or beetles, and allowed the investigator to concentrate only on airborne volatiles that the beetles could

potentially smell. Porapak Q methodology and gas chromatography (GC) have now become so sophisticated that volatiles from a single beetle can be captured and analyzed (Gries and others 1988; Birgersson and Bergstrom 1988). Coupled GC-mass spectroscopy (MS) (Rudinsky and others 1973), chemical derivation of chiral compounds prior to separation by GC (Slessor and others 1985), and chiral GC columns (Schurig and others 1982, 1983) have made it much easier to identify the correct geometrical and optical isomers of many scolytid pheromones.

Since the development of the original laboratory bioassay apparatus to assess the upwind responses of walking beetles to airborne olfactory stimuli (Wood and Bushing 1963), there have been many modifications. These include: (1) arrestment of beetles passing through or over a volatile stimulus (Kliefoth and others 1964; Jantz and Rudinsky 1965; Borden and others 1968a); (2) stimulation of walking in response to a light stimulus followed by deviation from the phototactic response when passing through an odiferous airstream (Borden and others 1968b); (3) arrestment of flying beetles on a rotary flight mill when a volatile stimulus is placed under the flight path (Borden and Bennett 1969); (4) 360° orientation in response to odors in a stationary flight mill (Hughes and Pitman 1970), and (5) mechanization of elution systems to provide a constant release of test volatiles (Payne and others 1976). Nonetheless, the beetles' responses are still of two types, positive anemotaxis toward an attractive source, or arrestment at or near a stimulus source. Generally, responses by pedestrian beetles have been good indicators of responses in nature by flying beetles. However, early doubts about the predictive capability of laboratory bioassays (Pitman and others 1966; Vité 1967) justifiably remain today, and verification of bioactivity by field bioassays is still considered essential.

Effective early traps for field bioassays were of three different designs: (1) a glass barrier fitted over a liquid-filled catching trough (Chapman and Kinghorn 1955); (2) an elaborate, sheet metal, tree-simulating device with volatiles from an internal bait dispersed up and out of a perforated metal column by means of a basal fan (Vité and Gara 1962); (3) or a wire mesh cylinder covered with a viscous sticky material and surrounding the test stimulus (Bedard and Brown 1969). The glass barrier trap was fragile and required frequent maintenance. The column olfactometer was heavy, expensive and required a power source, but provided a strong, vertical visual stimulus. The sticky trap was portable and relied on passive or active release of volatiles, but offered a poor visual stimulus, required laborious removal of captured beetles, and rapidly grew unpopular as field workers themselves became sticky. Some of the modifications that occurred over the years were: sticky panels (Barger 1979); bogus trees made of stovepipes (Atkinson and Wilkinson 1979) or drainpipes (Klimetzek and Vité 1978); a metal barrier, with forced air stimulus emission that fits around a tree (Gara 1967); perforated buckets (Moser and Browne 1978); cylindrical or flat barriers over a collecting funnel (Klimetzek and others 1981); and the employment of sticky vanes to increase trap surface area (Browne 1978).

Gradually inventors developed a series of traps that combined good visual stimulus, passive release of volatiles, light weight, small size, and capture of attracted beetles in a detachable receptacle. These took various forms and descriptive names, such as the drainpipe trap (Bakke and others 1983), the schlitzfalle trap (Staack 1985; Niemeyer 1985), and the multiple funnel trap (Lindgren 1983). Captured insects were originally immobilized in the receptacle below the trap in water with a surfactant added to break the surface tension (Chapman and Kinghorn 1955). Because this mix of water and putrifying insects rapidly became unpleasant and the insects hard to count, receptacles were modified to trap the beetles dry, often with the aid of a volatile insecticide to kill both the captured bark beetles and the predators that might otherwise have eaten them. The recently invented puddle trap (Byers 1993) appears to be a regression.

The technology for improving devices for controlled release of bark beetle semiochemicals has kept pace with the development of trapping technology (Borden 1982). Additional information on development of controlled release technology since 1982 can be found in many of the references in this paper.

Identity and Biological Role of New Semiochemicals

Research on the chemical ecology of bark beetles has resulted in identification of a number of unique new semiochemical compounds. These include: monoterpenes (Bedard and others 1969; Renwick and Vité 1969); terpene alcohols (Silverstein and others 1966); terpene ketones (Renwick 1967; Renwick and Vité 1969; Teale and others 1991); bicyclic ketals (Silverstein and others 1968); spiroacetals (Francke and others 1977, 1979); and fatty acid eaters (Byers and others 1988). The discovery of these new compounds has in turn challenged the talents of synthetic chemists throughout the world.

The first, tentative attempts to characterize the role of new semiochemicals in nature did not always yield anticipated results. This is because scientists were attempting to elucidate extremely complex and fascinating systems. The discoveries that were made were quite remarkable and have greatly enriched the study of chemical ecology. The concept of multicomponent blends to convey a species-specific, semiochemical-based message was first conceived for bark beetles (Silverstein and others 1966). Other discoveries made during the course of research on bark beetle semiochemicals include the elucidation of: synergism between host plant kairomones and insect-produced pheromones (Bedard and others 1969); antiaggregation pheromones (Renwick and Vité 1969); the role of juvenile hormone in stimulating pheromone production (Borden and others 1969); the curious role of multifunctional pheromones that have one function (for example, attraction) at a low concentration, and another function (such as repulsion) at a high concentration (Rudinsky 1973); the concept of mutual inhibition based on interspecific synomones (Birch and Wood 1975; Birch and others 1977, 1980); the role of geometrical isomerism (Silverstein and others 1966; Pitman and others 1968), optical isomerism (Wood and others 1976; Birch and others 1977, 1980), or both (Camacho and others 1993), in regulating response level

and species-specificity of pheromone channels; the kairomonal response of entomophagous insects to the aggregation pheromones of their bark beetle hosts (Bedard 1965; Bedard and others 1969); the stimulation of pheromone release in response to a sonic signal (Rudinsky and others 1973); and the role of microorganisms in pheromone synthesis (Brand and others 1975, 1976).

The functional role of bark beetle semiochemicals in nature demands an unconventional but realistic nomenclature (Nordlund 1981), such as the rule of one semiochemical, one name. How can one call a message-conveying blend a "pheromone" if one component of the blend is a host-produced kairomone? How can one call a beetle-produced blend a "pheromone" if one component is multifunctional, causing the blend to have different functions as the relative concentration of one of its components changes? The only realistic solution to this problem in the bark beetle world is to label each component by its functional role: aggregation pheromone, antiaggregation pheromone, multifunctional pheromone, synomone, or host plant kairomone. By this rule of terminology, a single compound can have more than one functional name. For example, an aggregation pheromone may also act as an interspecific synomone of mutual benefit to two species in maintaining reproductive isolation, or, an aggregation pheromone may act as an interspecific attractive kairomone for entomophagous insects.

Promise and Pitfalls in Developing New Semiochemicals for Use in Pest Management Tactics

Armed with knowledge of the identity and mode of action of bark beetle semiochemicals, and in possession of synthetic material of high purity and authenticity, the courageous investigator will try out these new materials, discovering what they are capable of doing in pest management. The results of these attempts were usually very encouraging in the past, and continue to be so today. Thousands of beetles can be attracted to traps (Browne 1978). Attack can be induced on semiochemical-baited trees (Dyer 1973). Attraction to traps or trees can be inhibited (Rudinsky and others 1972; Borden and Lindgren 1988). Natural enemies can be attracted in large numbers (Chatelain and Schenk 1984). The temptation was great to launch immediately into ambitious research and development (R and D) projects, and oversell the practical promise of bark beetle semiochemicals.

But bark beetle semiochemical systems are tremendously complex, biologically and chemically. While such complicated systems can offer numerous opportunities to exploit them (Borden 1989), they also can foil the pest manager who does not understand their natural complexity. Superimposed on these biological and chemical challenges are the additional challenges of making the right judgements as to the most effective R and D protocol, and fitting whatever tools are needed into the biological, economic, and social contexts in which they will be used optimally.

Two examples, one on the use of attractive pheromones and kairomones, and the other on an antiaggregation pheromone, illustrate how the development of semiochemical-based pest management tactics can go astray.

The very first, and most promising, trial of mass trapping against the western pine beetle (*Dendroctonus brevicomis* LeConte), at Bass Lake, CA, in 1970 (Bedard and Wood 1974) is an illuminating example of imperfect R and D. The small, isolated infestation in a forest of very high social value was a well-chosen target for a test of an intensive pest management tactic. A great effort was made to have trap-out, survey, and control areas; to monitor populations as well as mass trap them; and to accurately assess the efficacy of the program. Mass trapping during the spring of 1970 apparently reduced the numbers of trees attacked in the next generation and for the following 2 years. However, the mass trapping effort was unfortunately stopped after only 3 months. Had the program lasted for a whole year, or if necessary longer, a true test of mass trapping to eradicate a bark beetle infestation might have been accomplished.

It might have been necessary to abolish the survey and control areas and apply a concerted mass trapping effort throughout the infestation. The results of this and other trials would then have been judged by repetition, until the historical record was sufficiently impressive to convince most skeptics that mass trapping actually worked. The avoidance of controls in operational R and D programs is a subject of frequent criticism, but repeated non-controlled trials may be better than not attempting to use semiochemicals at all. I am in agreement with repeated, uncontrolled trials of the use of integrated cut and repel tactics against spot infestations of the southern pine beetle (*Dendroctonus frontalis* Zimmerman) (Payne and others 1992).

Unfortunately, there have been no repetitions of mass trapping trials against small, constrained infestations of the western pine beetle similar to that at Bass Lake, and few or none for other species. This has been due to a lack of either opportunity or commitment by operational researchers. Those mass trapping programs that have been attempted were against populations so large that massive technical and logistical challenges apparently overwhelmed the trapping efforts. For example, mass trapping of the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham), in heavily infested areas, failed to suppress the target populations adequately (Lanier and others 1976; Birch and others 1981). Mass trapping is recommended only as one component of a Dutch elm disease management program that also involves sanitation and other management tactics (Lanier and others 1976).

It is not surprising that the largest, mass trapping effort ever, which used 605,000 and 650,000 drain pipe traps in Norway and Sweden in 1979 and 1980 (declining to 220,000 traps in 1983) to capture over 11 billion European spruce beetles, *Ips typographus* L., produced equivocal results. After the infestation subsided Bakke (1983, 1989) concluded that suppression of the outbreak was caused by cool, wet weather, recovery of resistance in the remaining trees, removal of infested trees and mass trapping.

Attempts to use the antiaggregation pheromone verbenone against the mountain pine beetle, *Dendroctonus*

ponderosae Hopkins, represent another example of imperfect R and D. There is no doubt that verbenone can effectively cause populations to disperse or not to aggregate (Amman and others 1989; Lindgren and others 1989; Shea and others 1992). However, the prospect of developing verbenone into a truly operational tool has been confounded by inconsistency in results from year to year or in different forest types or geographic regions.

The periodic failures could be due to technical problems involving the deployment, persistent release, and dispersion of verbenone, as well as the influence of microclimate, weather, and even genetic changes in the target insect (Amman 1993). They could also be due to a lack of comprehension of how verbenone works in nature. Consequently applications are misdirected with regard to forest type, geographic location and target population, or inadequate in strength, timing, or position. One possible reason for ineffective treatments is the photodecomposition of verbenone to an inactive compound chrysanthenone (Kostyk and others 1993). Such natural breakdown would prevent widespread verbenone-based disruption from occurring in nature. In practice, it could greatly reduce efficacy in forests with sparse crown closure, growing in warm, sunny climates, as is characteristic of many stands of ponderosa pine (*Pinus ponderosa* Laws.) (Gibson and others 1991).

Inconsistency in effectiveness would lead to reluctance of a responsible manufacturer to produce and sell verbenone for operational application in a small, uncertain market. It would also lead to forest pest managers being reluctant to rely on verbenone applications to control a mountain pine beetle problem. The efficacy of verbenone may be improved by combining its application in one area with an attractant deployed in an adjacent area in a "push-pull" tactic (Lindgren and Borden 1993). Another is to deploy it in combination with another antiaggregant, such as an interspecific synomone that mediates species specificity in semiochemical communication (Paine and Hanlon 1991), or with green leaf volatiles that might convey a false message for example, the stand in question was a non-host species (Dickens and others 1992).

Operationally Successful Applications of Semiochemicals

Despite the difficulties inherent in planning, guiding and evaluating R and D, there is ample evidence that many efforts have reached sufficient maturity to graduate to the status of operational implementation or readiness (Borden 1993). These applications include: (1) containment and concentration of mountain pine beetle and spruce beetle populations prior to logging by baiting uninfested trees at 50-m centres prior to emergence and flight (Borden 1990; Shore and others 1990); (2) predicting an increase or decrease in southern pine beetle population levels by assessing changes in the ratio of predators to prey captured in semiochemical-baited traps (Billings 1988); (3) using sticky traps or baited trees to monitor emergence trends and population levels of mountain pine beetles to decide when to impose no-haul restrictions (Stock 1984) or basal applications of an arsenical herbicide to newly-infested trees

(Hall 1989); (4) combining tree baiting with basal applications of an arsenical herbicide to reduce populations of smaller European elm bark beetles (Lanier 1989) and mountain pine beetles (Hall 1989); (5) combining tree baiting with application of insecticidal sprays to the bole surface against western pine beetles (Smith 1986); (6) employing synomones of two competitor species to deter attack by pine engravers, *Ips pini* Say (Borden and others 1992; Miller and others 1993); (7) prevention of attack by widespread application of antiaggregation pheromone against the Douglas-fir beetle (Furniss and others 1981, 1982); (8) combined applications of antiaggregation pheromone with silvicultural treatments against the southern pine beetle (Payne and others 1992); and (9) push-pull control of the California fivespined ips using repellent synomones and attractive pheromones (Berson 1992; Shea, these proceedings).

Prospects

Finally, it is interesting to contemplate how the next generation of semiochemical-based tactics against bark beetles will be conceived, developed, and applied. I predict that the next generation of semiochemical-based strategies and tactics against bark beetles will be profoundly influenced by innovation and sophistication in three areas: (1) conventional technology, (2) biotechnology, and (3) applied ecology.

We have done very well with conventional technology. Nonetheless, it is probable that in the future we will see even better and cheaper methods of chemical identification and synthesis, better controlled release devices, and more effective, durable, and portable traps. Semiochemicals for most species remain unknown. There are strong suspicions that one or more critical semiochemical components for species already studied are yet to be discovered. A key technology that may lead to the discovery of new semiochemicals in the future is the use of coupled gas chromatographic-electroantennographic detection (Gries, these proceedings).

Application of biotechnology in the future will surely include much more use of enzymatic synthesis to produce chirally pure semiochemicals (Ramaswamy and Oehlschlager 1989). Some of these syntheses may be achieved *in vitro* by engineered microorganisms. We may in the distant future witness the planting of genetically engineered trees that emit antiaggregation pheromones or convey messages (perhaps through green leaf volatiles) that they are of the "wrong" host species.

Pest management is an increasingly prominent field of applied ecology. To date applications of semiochemicals against bark beetles have been restricted largely to single messages targeted to single pest species on single host species. I contend that the use of bark beetle semiochemicals will increasingly be integrated with community and ecosystem management. Managed forests will contain a diversity of tree species growing with such vigor that even aggressive bark beetles will be defeated. Applications will increasingly incorporate multiple tactics using semiochemicals of diverse functions targeted against two or more species. They may attempt to induce competitive displacement

of major pest species with secondary species (Payne and Richerson 1985; Rankin and Borden 1991; Borden 1992) or enhance the impact of natural enemies (Schroeder and Weslien, in press). When infestations occur that demand management, semiochemicals will be applied as part of well developed integrated pest management programs (Safranyik and Hall 1990). Semiochemical-based tactics will represent a small, but critical, number of the total possible tactics to be selected for operational use.

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Management Potential of Semiochemicals for Protection of Trees from Western Pine Beetle

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Abstract—The components of the semiochemical communication system of the western pine beetle, *Dendroctonus brevicomis* Le Conte (Coleoptera: Scolytidae), have been well characterized. *Exo*-brevicomin and frontalin function as attractant pheromones, while the pheromones verbenone and ipsdienol appear to have inhibitory effects. Recent research demonstrates that a combination of verbenone and ipsdienol appear to be additive in inhibitory effect. The potential of using the inhibitory pheromones to protect standing ponderosa pines was tested by placing verbenone and ipsdienol on trees baited with aggregation pheromones. Beetle landing and attack rates were significantly reduced on inhibitor-treated trees compared to trees with aggregation pheromone alone.

Pheromone-Based Management of Bark Beetles

Like many other tree-killing scolytids, the western pine beetle, *Dendroctonus brevicomis* Le Conte (Coleoptera: Scolytidae), produces pheromones that stimulate arrival of large numbers of beetles on host trees within short periods of time (Wood 1972). Females initiate colonization of trees and produce *exo*-brevicomin (Silverstein and others 1968). Arriving males produce frontalin (Kinzer and others 1969). The response of beetles to these pheromones is synergized by host volatiles, particularly the host monoterpene myrcene (Bedard and others 1969).

The colonization process is terminated as a result of several factors, including cessation of production of the aggregation pheromones (Raffa and Berryman 1983) and production of antiaggregation or inhibitory pheromones. Verbenone, produced by beetles (Byers and others 1984) as well as by microorganisms (Brand and others 1974) and through auto-oxidation of α-pinene (Hunt and others 1989), is inhibitory to *D. brevicomis*, as is ipsdienol (Paine and Hanlon 1991), which is produced by male beetles (Byers 1982; Byers and others 1984) and by both *Ips pini* (Say) (Birch and others 1980) and *I. paraconfusus* Lanier (Silverstein and others 1966). Although the *Ips* species

produce opposite enantiomers [*I. pini* produces (−) ipsdienol (Birch and others 1980), *I. paraconfusus* (Silverstein and others 1966) and male *D. brevicomis* produce (+) ipsdienol (Byers 1982; Byers and others 1984)], both sexes of *D. brevicomis* are inhibited by racemic mixtures of ipsdienol (Paine and Hanlon 1991).

It was not long after pheromones were identified in bark beetles that their potential for use as management tools was explored. However, the implementation of pheromones into applied programs has lagged behind. In part, this may be due to a problem of focus or perception of management goals. There are two goals that, although similar, are different in the way management programs are executed. If a management goal is to reduce population levels of a damaging pest, the result may or may not be a reduction in tree mortality unless the populations are reduced below a critical level. If a management goal is to reduce tree mortality, this may be accomplished without reducing the population. In addition, both of these goals must be focused on either protection of stands or individual trees.

Protection of stands of trees by reducing beetle populations using attractant pheromones in a mass trapping program received early attention (Wood 1982; Bakke 1988). More recently, the use of attractant pheromones has been integrated with the use of inhibitors. Flying beetles have been diverted out of high value stands and attracted into areas that are easily harvested or are poor resources for beetle reproduction (Borden and others 1986; Payne and Billings 1988).

Modified approaches using the same concepts can be implemented for single tree protection. Inhibitors can be applied to high value trees prior to beetle activity and maintained throughout the flight season to reduce the risk of beetle attack. However, the efficacy of this approach has received minimal attention.

Current Western Pine Beetle Research

Paine and Hanlon (1991) demonstrated that both verbenone and ipsdienol inhibited response of *D. brevicomis* when each was released in conjunction with the beetle's aggregation pheromone, but the combination of both inhibitors released together produced a significant further reduction in response. Bertram (1993) investigated the effect of release rate of inhibitors and the ratio of inhibitors to attractant pheromones on the response of flying beetles. She showed that release rates of ipsdienol as low

as 0.09 mg/24 hr significantly reduced response of *D. brevicomis*, but similar reductions were not observed at these extremely low rates of 14 percent (+)/ 86 percent (−) verbenone. Low rates of the combination of verbenone and ipsdienol were inhibitory and the effect of the two inhibitors released together may possibly have been additive. Further investigations of release rates and release ratios of verbenone to attractant pheromones indicated that ratios of attractants *exo*-brevicomin and frontalin to verbenone of 1:4 or greater inhibited responding beetles. Similarly, total release rates of verbenone above 6.0 mg/24 hr were critical for inhibition of beetle response to aggregation pheromones.

Bertram (1993) also tested the use of ipsdienol plus verbenone to protect individual trees from *D. brevicomis* attack. Trees were baited with aggregation pheromone and half of the trees also were treated with inhibitors. Release devices containing verbenone or ipsdienol were alternated at 0.5-m intervals from ground level to 5.0 m up the trunk and a bait containing aggregation pheromone was placed at 2.0 m above the ground. Trees with the inhibitor treatment had fewer beetles land on the trunk and fewer attacks compared to trees baited with the attractants alone. However, the results from this trial did suggest that once beetles arrive at a tree, the treatments with verbenone and ipsdienol did not decrease the likelihood that they would initiate an attack. Thus, it appears that inhibition occurs prior to landing rather than on the bark surface. By necessity, the study used a destructive sampling technique that required trees be felled. It is not clear whether the inhibitor-treated trees would have survived western pine beetle attack. However, during the period of time when attractant pheromones were on the trees, the attack density did not exceed the critical threshold of 1 attack /100 cm^2 proposed for *Dendroctonus frontalis* colonizing loblolly pine (Hodges and others 1979). Although the threshold for attack may be different for different beetle species or for trees of different size, species, or growing at different levels of vigor, low attack densities or slow attack rates may enable the natural resistance of vigorous trees to prevent successful beetle colonization (Paine and others 1984).

Conclusions

Previous research with pheromones of *D. brevicomis* has indicated that there may be a significant potential for use of these compounds for reduction in tree mortality but that the implementation of the research into applied management is difficult. More recent work has suggested that management programs that incorporate attractants and inhibitors may have significant advantages. We have recently demonstrated that landing rates and attack densities can be greatly reduced on individual attractive trees. The labor and chemical costs are currently expensive and would require that the release devices currently available be changed several times during the flight season. The technical problems involved with producing release devices that remain active for longer periods of time and can be

easily placed along the entire length of the trunk should be resolved before devices can be made commercially practical. However, use of inhibitors appears to have a good potential for protecting high value trees and warrants further exploration.

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Semiochemicals for Management of Mountain Pine Beetle: Status of Research and Application

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Abstract—Semiochemical research has led to the operational use of aggregation pheromones for management of the mountain pine beetle, *Dendroctonus ponderosae*, particularly in British Columbia. Extensive research has been conducted to investigate the use of the antiaggregation pheromone, verbenone, as a potential management tool. Initial research provided encouraging results, but more recent experiments yielded ambiguous data. Many potential problems with verbenone have been identified. Current research is investigating the use of other repellant compounds as synergists to verbenone.

The main pheromones of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, (Coleoptera: Scolytidae), have been known for many years (Borden 1982; Lindgren and Borden 1989). Advances in their synthesis and formulation in slow release devices during the past 10 years have led to considerable experimentation in operational scale applications for beetle population management and protection of stands and individual trees from infestation.

The mountain pine beetle is indigenous to the Western United States and Canada. It infests 13 species of pine native to North America (Wood 1982) as well as exotic pine species. Lodgepole pine, *Pinus contorta* Douglas, is the principal host of mountain pine beetle. Populations of the beetle periodically build up and kill most of the large dominant lodgepole pines over vast areas. The large trees usually have thick inner bark (phloem), which is the food of developing larvae, enabling good survival and high brood production. Frequency of infestations in a given area of forest appears to range from about 20 to 40 years (Roe and Amman 1970), depending on how rapidly some trees in the stand grow to large diameter and produce thick phloem, conditions conducive to buildup of beetle populations. During outbreaks, beetles may kill 70 to over 90 percent of the lodgepole pines 13 cm and larger in diameter at breast height (dbh) (McGregor and others 1987).

The mountain pine beetle usually completes one generation per year in lodgepole pine. However, 2 years may be required at high elevations and in the cooler climates of northern latitudes. New adults, which are about 5 mm long, emerge from the bark and attack live trees between late June and early September, depending on elevation, latitude, longitude, and local weather conditions (Bentz and others 1991; Rasmussen 1974; Reid 1962; Safranyik and others 1974).

The mountain pine beetle has an elaborate pheromone communication system that governs its attack behavior (Borden and others 1987; Lindgren and Borden 1989). At the onset of attack by female beetles, the host monoterpenes α-pinene and myrcene, together with female-produced *trans*- and *cis*-verbenol (Miller and Lafontaine 1991), attract primarily male beetles to the tree. As males reach the tree they release *exo*-brevicomin, which attracts primarily females, thereby enhancing the level of attraction. As additional males colonize the tree, attractiveness is reduced as concentrations of *exo*-brevicomin and frontalin increase (Borden and others 1987). Simultaneously, concentrations of the aggregation pheromones, *trans*- and *cis*-verbenol, and host monoterpenes begin to decline. At this stage in colonization, increasing concentrations of verbenone produced (1) by autoxidation of the host monoterpene, α-pinene, to *trans*- and *cis*-verbenol and then to verbenone (Hunt and others 1989), and (2) by conversion of verbenols to verbenone by microorganisms (Hunt and Borden 1989), deter additional beetles from attacking the focus tree. The effect of these antiaggregation pheromones limits attacks to a density that ensures survival of the ensuing brood. Beetles switch to adjacent trees where the process is repeated (Geiszler and Gara 1978).

Following mating, females lay eggs in irregularly alternating groups on the two sides of the vertical gallery within the phloem near the xylem. Eggs hatch in about 2 weeks and larvae feed individually in the phloem. Larval galleries usually extend at right angles to the egg galleries, thereby girdling the tree. There are four larval instars. Larvae usually pass the winter most successfully in larger instars. When mature in late May and June, larvae excavate oval cells in the phloem, lightly scoring the sapwood, where they pupate and become adults. New adults feed within the bark prior to chewing exit holes through the outer bark and then emerge to attack live trees and repeat the cycle.

Research and Application of Aggregation Pheromones

Trapping

Detection trapping is generally done for quarantine purposes. The objective is to detect species that are perceived as potential threats to particular resources.

During epidemics there is a real risk of long range spread of mountain pine beetles. For example, mountain pine beetle appeared in the Cypress Hills area on the border of Alberta and Saskatchewan in Canada, as well as in ornamental and shelter belt pine plantations throughout southern Alberta in the 1980's (Cerezke 1989). The closest source of beetles was the Glacier National Park area in Montana and the adjacent Waterton Lakes Park in southeastern Alberta, some 200 km to the west. Introductions of mountain pine beetle to Eurasian pine forests could have potentially devastating consequences. Mountain pine beetles have been intercepted in New Zealand (Marchant and Borden 1976), demonstrating the potential of accidental introductions.

There are no programs in North America using pheromone traps for detection of the mountain pine beetle in areas outside its natural range. A limited number of traps are employed by the Forestry Commission in Great Britain for detection of mountain pine beetles (40 traps), the Douglas-fir beetle, *Dendroctonus pseudotsugae* (40 traps), and the European spruce bark beetle, *Ips typographus* (100 traps). So far no interceptions of either *Dendroctonus* species have been made (Burgess 1994).

Monitoring involves trapping with the objective of determining specific characteristics in the population dynamics of an insect species. The use of semiochemicals for monitoring bark beetle flight has been a recognized operational procedure in British Columbia for many years (Hall 1989; Province of British Columbia 1985), and several Forest Districts use pheromone-baited traps on a routine basis to determine the timing of the major mountain pine beetle flight. In the basis of this information, hauling bans from infested areas are implemented (Hall 1989; Stock 1984). No rigorous attempts at correlating catches with population densities have been made.

Mass trapping is the use of traps for actual population suppression. It was attempted for mountain pine beetles in 1984 by the U.S. Department of Agriculture, Forest Service in Montana and Idaho (Steele 1988). Lindgren funnel traps were placed in grids or clumped in infested stands. While statistical analyses of tree mortality data apparently provided some weak evidence for an effect due to the trapping, populations in all stands were generally declining during this trial. No further mass trapping attempts were made.

As with many other bark beetle species, the use of pheromone-baited traps for mountain pine beetles frequently results in extensive spillover attacks on trees near the traps. Until a more powerful attractant is identified, allowing placement of traps away from susceptible host trees, as is done in Europe for *Ips typographus* (Weslien 1992), there is probably little or no potential for mass trapping as a management tool for the mountain pine beetle.

Tree Baiting

Tree baiting was developed and refined as a management technique in British Columbia in the early 1980's (Borden 1990 and references therein). It has been operationally employed in British Columbia since the mid-1980's, and is a recognized operational procedure by the British Columbia Ministry of Forests (Province of British Columbia 1987; Hall 1989). In a recent document, extensive use of tree baiting was recommended as operational tactics for three of six mountain pine beetle management strategies in the Okanagan Timber Supply Area (Safranyik and Hall 1990). In the United States the technique has been tested (McGregor and others 1989), but has been implemented only on a very limited scale. Tree baits have been exempted from registration by the Environmental Protection Agency in the U.S., and their use is monitored in Canada while registration guidelines for so-called biorational pesticides are developed.

Tree baiting is not a control treatment in itself, but rather a tool designed to enhance the use of other direct control tactics. In fact, in the absence of harvesting or other follow-up control treatment, tree baits may exacerbate the beetle problem since both attack densities and tree mortality are increased where baits are used. In concert with silvicultural or other treatments, tree baits offer an effective means of predetermining where treatment efforts should be located; this substantially reduces the costs associated with ground probes needed to determine infestation spread (Hall 1989).

Tree baiting is normally done by ground crews during May and June, and sometimes July, the months prior to the mountain pine beetle flight. Baits are attached on the north sides of susceptible trees as high as the applicator can reach. A trained crew can bait a stand in this fashion fairly quickly.

There are four operational applications for tree baits for mountain pine beetle management: (1) detection and monitoring, (2) containment and concentration, (3) postlogging mop-up, and (4) spot suppression.

Tree baits can be used for detection and monitoring of mountain pine beetle populations. The drawback is that attacked trees must be destroyed. Nevertheless, tree baits are used for monitoring purposes in British Columbia. The Fort St. John Forest District used between 450 and 750 baits per year for this purpose between 1991 and 1993 (Hodgkinson 1993). Baits were used extensively in Alberta and Saskatchewan from 1983 to aid in the detection and monitoring of mountain pine beetle populations in lodgepole pine and limber pine stands (Cerezke 1989).

The objective of the containment and concentration tactic is to prevent dispersal of mountain pine beetles from infested stands, while maximizing immigration into and arrestment within the baited stand by beetles dispersing from surrounding areas. Baits are generally applied in a 50- by 50-m grid throughout the stand, leaving a 25-m buffer at the edge. For exceedingly large blocks, perimeter baiting may be an option. This will reduce the cost per ha by preserving baits. The objective of perimeter baiting is to prevent dispersal out of the infested block.

The objective of the post-logging mop-up tactic is to concentrate beetles left behind after harvesting. Beetles

emerging from stumps, logging slash, or isolated infested trees beyond the cut block boundaries, can be attracted to predetermined areas, where they can be disposed of through additional limited harvesting, or by single tree treatment. In this manner residual populations can be held in check or eradicated, reducing risks for future population buildup.

The use of the herbicide monosodium methyl arsenate (MSMA) as a treatment of infested trees for spot suppression has become routine in inaccessible areas and stands where silvicultural or harvesting treatments cannot be used (Hall 1989). Tree baits have made this technique efficient and cost effective. The objective is to prevent reproduction in attacked trees. Susceptible trees are baited prior to mountain pine beetle flight. Shortly after attack, MSMA is applied to axe frills at the base of attacked trees (hack-and-squirt application). The MSMA applied within the prescribed 3-week window, when the pesticide is translocated throughout the tree, leads to the phloem tissues rapidly drying out; this in turn effectively prevents beetle reproduction.

Competitive Displacement

Resource partitioning on the basis of interspecific competition is a common phenomenon among bark beetles. Recent studies have shown that synthetic pheromones of competing (secondary) bark beetle species may disrupt aggregation, enhance the effect of antiaggregation pheromones such as verbenone, or induce attacks by the secondary species causing reproductive failure of the target species. Several secondary bark beetle species share lodgepole pine with the mountain pine beetle as a breeding resource (Furniss and Carolin 1977). The main competitor is the pine engraver, *Ips pini*, which frequently occupies the upper bole of mountain pine beetle infested trees.

Hunt and Borden (1988) found that ipsdienol, the principal aggregation pheromone of *I. pini*, significantly reduced catches of mountain pine beetles in traps baited with *trans*-verbenol, *exo*-brevicomin and myrcene. Safranyik and others (1993) found that simultaneous baiting of lodgepole pine with the aggregation pheromones for mountain pine beetles, and ipsdienol and lanierone, the aggregation pheromones of *I. pini*, resulted in significant reductions in mountain pine beetle attack, egg gallery, and brood densities.

Using ipsdienol, Rankin and Borden (1991) induced attacks by *I. pini* on trees recently infested by the mountain pine beetle, resulting in a 72.5 percent reduction in mountain pine beetle progeny, compared to untreated control trees. Safranyik and others (1994) used ipsdienol and lanierone to induce *Ips* spp. attacks on lodgepole pines at different times following mountain pine beetle attack. In this experiment the effect on mountain pine beetle reproduction was marginal.

Applications of Antiaggregation Pheromones

The antiaggregation pheromones that have been identified for mountain pine beetles are verbenone, *exo*-brevicomin

at high release rates, frontalin at high release rates, and ipsdienol. Of these, verbenone appears to be the most promising for practical applications.

Beetle Response to Attractive Traps

Ryker and Yandell (1983) tested the effect of a "high" release rate (0.08 mg/24 h) of racemic verbenone around sticky traps baited with *trans*-verbenol and monoterpenes. Mountain pine beetle catch was reduced by 87 percent, or to the level of blank control traps. Verbenone released at a "low" rate (0.001 mg/24 h) did not have a significant effect on trap catch.

Schmitz and McGregor (1990) conducted tests in Northern Utah in 1986 to assess the response of mountain pine beetles to funnel traps baited with *trans*-verbenol, *exo*-brevicomin, and myrcene with or without verbenone released at 5 mg/day at 25 °C. Overall, the addition of verbenone to the synthetic mountain pine beetle lure reduced the catch by 98 percent.

A similar test in British Columbia by Borden and others (1987) showed that when verbenone was released at 1 and 5 mg/24 h, respectively, in funnel traps baited with the attractive synthetic mountain pine beetle lure, the response of males was reduced by approximately 75 percent. Female response was reduced similarly, but not significantly.

The encouraging results from these studies prompted tests to determine the efficacy of verbenone for reducing mountain pine beetle infestation in lodgepole and ponderosa pine, *P. ponderosa* Lawson, stands, and on individual lodgepole pines.

Ground Tests in Lodgepole and Ponderosa Pine Stands

Field studies to test the efficacy of verbenone in reducing mountain pine beetle infestation in stands were conducted in Idaho, Montana, and British Columbia, starting in 1987. Two experiments were conducted in British Columbia (Lindgren and others 1989). The first experiment compared (1) mountain pine beetle tree bait, and (2) tree bait and verbenone; the second compared (1) untreated control and (2) verbenone alone. In Idaho, all four treatments were compared in one experiment (Amman and others 1989). Each treatment was applied individually to 1-ha plots, except in the second experiment in British Columbia, which used 4-ha plots. Five mountain pine beetle tree baits were used in each baited plot, and verbenone plots were treated with 100 verbenone bubble capsules per ha applied on a 10- by 10-m grid.

The results from these two independent studies were remarkably similar. There was no significant difference between control and verbenone plots in either study, but highly significant effects were achieved by verbenone compared to the baited plots.

Percent reduction in mountain pine beetle-caused mortality

	Bait vs. verbenone + bait	Control vs. verbenone
Idaho	74.1	74.3
British Columbia	74.3	75.2

These encouraging studies led to additional studies in 1988 and 1989 to determine the relationship between verbenone dose and mountain pine beetle response in lodgepole pine stands of Idaho (Amman and others 1991), Montana (Gibson and others 1991), and British Columbia (Safranyik and others 1992).

In Idaho and Montana, five treatments consisting of different numbers of verbenone bubble caps (0, 25, 49, 100, and 169 caps/ha) were applied in grid patterns within plots in 1988. In addition, each plot had two 20-m wide strips established around the perimeter to determine if beetle infestation increased in the area immediately adjacent to verbenone treated plots (Amman and others 1991). The 1989 test was similar to the 1988 test except strips were not used around the plots. In 1988, treatments were replicated seven times and in 1989 they were replicated eight times.

All verbenone doses reduced tree mortality within treated plots in both years when compared to untreated control plots. There was a trend of lower mortality with increasing verbenone dose in both years. However, the highest dose sustained higher mortality than the intermediate doses. In the strips surrounding verbenone treated plots in 1988, there were no significant differences in number of trees mass attacked. However, the trend was for fewer infested trees as quantity of verbenone increased in the plots (Amman and others 1991).

In the Montana studies (Gibson and others 1991), designs were similar to those used in Idaho. In 1988, treatments were not significantly different. However, in 1989, treatments were significantly different, and the results were very similar to those in Idaho. As in the Idaho test, the 100 capsules/ha treatment showed the greatest reduction in percent of infested trees, with a mean of 0.3 percent compared to check plots that had a mean of 5.2 percent. The lack of significant treatment effect in 1988 was attributed to the low number and poor distribution of infested trees among plots. The average percentage of infested trees ranged between 0.2 and 2.5 when the study was installed.

Bentz and others (1989), Gibson and others (1991), and Lister and others (1990) used methods similar to those described in the previous section for lodgepole in Idaho to test the effect of verbenone in ponderosa pine stands in southwestern Colorado, in western Montana, and in western South Dakota. Tests were not successful.

Mountain pine beetle infestations in these areas were in outbreak status, but the intensity of the infestations was much higher in southwestern Colorado, where over 150 trees per hectare were killed in 1988 (Bentz and others 1989). In the outbreak cycle, the Colorado area was considered at its peak; the South Dakota area was in the early stages of an outbreak (22 infested trees/ha), and the Montana area was intermediate (32 infested trees/ha).

In each area, as in the lodgepole pine test, four replicates were used to test the five treatments; 0, 25, 49, 100, and 169 verbenone bubble caps/ha (elution rate 5mg/day/capsule at 25 °C). In 1988, no significant differences occurred among treatments in any of the areas. The numbers of mass-attacked trees in the strips surrounding the plots also were not significantly different among treatments, nor different from those within the plot.

In 1989, eight replicates were used to again test different verbenone treatments in South Dakota and Montana. Mountain pine beetle populations had reached outbreak status, but the population trend was static in South Dakota (11.6 infested trees per hectare) and in Montana (11.0 infested trees per hectare).

Both the South Dakota and Montana tests showed a downward trend in infestation with increased number of verbenone capsules, but due to high variance within treatments and low number of replicates, significant treatment effects could not be demonstrated.

The results from the dose response experiments in lodgepole and ponderosa pine are similar (fig. 1), in spite of the fact that statistical significance was not obtained in several of these experiments. The general trend of reduced mortality as a function of verbenone dose is consistent with dose-dependent response by the mountain pine beetle in trapping experiments (Miller and others in press). Even in the experiment in ponderosa pine in Colorado, where extremely high beetle populations probably precluded any possibility of a significant verbenone effect (Bentz and others 1989), and in one experiment in lodgepole pine in Montana, where control mortality was only 0.3 percent (Gibson and others 1991), there were slight (non-significant) reductions in mean mortality in treated blocks compared to controls.

Safranyik and others (1992) tested two release rates of verbenone for effects on mountain pine beetle dispersal, landing, and attack behavior in lodgepole pine stands. The two release rates were either one or two bubble caps attached to trees on a 10- by 10-m grid. Unbaited landing traps were placed on lodgepole pines in a 10- by 10-m
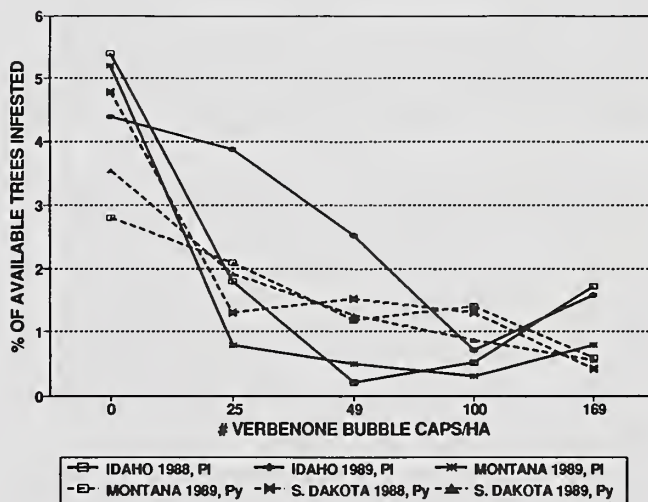

Figure 1—Comparison of results from verbenone dose experiments in lodgepole pine (solid lines) and ponderosa pine (dashed lines). Graph generated from data by Amman and others 1991 (Idaho 1988 and 1989), Gibson and others 1991 (Montana 1989), Bentz and others 1989 (South Dakota 1988), and Lister and others 1990 (South Dakota 1989). Pl = Lodgepole pine, Py = Ponderosa pine.

grid. Infested log sections dusted with different colored fluorescent dyes were positioned in the middle of each 100- by 100-m block to assess beetle movement in relation to verbenone applications.

There was no significant difference between the two verbenone treatments for number of attacked trees, or number of attacking beetles. However, the means of all experimental variables were lower in verbenone-treated plots than control plots. The difference in number of beetles trapped was statistically significant at $\alpha = 0.1$, with more marked beetles caught in the control than verbenone-treated plots.

L. Rasmussen (USDA Forest Service, Logan, UT, personal communication) established studies in 1990 and 1991 in Central Idaho to determine whether 49 or 100 bubble capsules of verbenone/ha were most effective in lodgepole pine, since each treatment had given the best results in previous tests (Amman and others 1991). A significant treatment effect was not shown either year when compared with controls, nor among verbenone rates, although significant effect of verbenone was shown for 1987, 1988, and 1989 (Amman and others 1989, 1991) for the same area in Idaho.

Rasmussen's results suggest that selection may be occurring for beetles that ignore or are attracted to the verbenone signal. In these studies most of the large diameter trees had been killed in previous years, leaving only smaller trees available for attack. In these trees, the larvae survival rate is usually lower than in large diameter lodgepole (Cole and others 1976) and beetles reared in thin phloem take longer to develop and are smaller in size (Amman and Cole 1983). Such beetles would be more typical of those found at low, non-outbreak population levels. Schmitz (1988) found that beetles in such populations tended to infest diseased trees and trees infested by secondary bark beetle species such as *Ips*, *Pityogenes*, and *Pityophthorus*. Low to moderate levels of verbenone produced by oxidation of pheromones and terpenes in such trees may attract the types of mountain pine beetles produced in poor host material, that is, trees of small diameter with thin phloem.

Aerial Application of Verbenone

Shea and others (1992) used verbenone formulated in controlled release, cylindrical, 5- by 5-mm plastic beads applied at the rate of 54 g verbenone per hectare from a helicopter in mountain pine beetle infested lodgepole pine stands of northwestern Montana. After treatment, the mean number of currently infested trees (1988) did not differ between treated and control plots. However, the control plots had four times as many infested trees as treated plots, and the mean ratio of 1988 to 1987 attacked trees per hectare was significantly higher in control plots than in treated plots. The mean number of unsuccessfully attacked trees per hectare was significantly higher in verbenone treated plots. Although these results were quite encouraging, a subsequent experiment failed to achieve the same response (P. Shea, USDA Forest Service, Davis, CA, personal communication).

Shea and others (1992) discussed the possible influence of stand microclimate as a factor affecting results of

verbenone tests. They found that verbenone eluted more rapidly from beads in open stands than from those in closed stands.

In a simulated aerial test of verbenone-impregnated beads, Kostyk and others (1993) observed that trap-catches of mountain pine beetle were 50 percent higher in traps hung above beads placed on the ground than in traps containing similar beads. They also found that 50 percent of verbenone vapors, when exposed to full sunlight, were converted to chrysanthenone in 75 and 100 minutes during two tests. Chrysanthenone had no influence on the response of mountain pine beetle to synthetic attractants.

The rate of photoisomerization of verbenone may vary according to geographic location, stand elevation, and density (Kostyk and others 1993). No chrysanthenone was found in bead samples from Idaho, but considerable amounts occurred in Montana samples (Lindgren 1991). In closed canopy samples, up to 36.7 percent of the sample was accounted for by chrysanthenone; in open canopy samples up to 51.5 percent.

Lindgren (1991) did a small aerial application test in conjunction with tests of verbenone bubble capsules in British Columbia. He used 4-ha plots replicated four times to compare 100 bubble capsules per hectare (80 g active ingredient/ha), aerial application of 2.8 kg of beads (84 g active ingredient/ha), and untreated control. He found that each verbenone application reduced infestation, but neither was statistically significant. Lack of significance was probably due to the small number of replicates and a treatment by replicate interaction. Nevertheless, treated plots had less than half the percentage of infested trees as the control plots, and almost twice the percentage of lightly infested trees (unsuccessfully attacked).

Push/Pull Strategy

The use of verbenone to repel beetles from one stand of trees, combined with aggregation pheromones to attract the beetles to an adjacent stand scheduled for logging was considered potentially the most operationally feasible tactic with pheromones (Borden and Lindgren 1989). Aggregation pheromones may shift infestations of mountain pine beetle (Borden and others 1983), as well as concentrate and contain them (Gray and Borden 1989). However, the maximum distance of attraction is considered to be 75 m (Borden and Lindgren 1988).

Lindgren and Borden (1993) designed an experiment to test displacement of beetles and their attraction to adjacent stands. Treatments were: (1) control, (2) verbenone in a central 50- by 150-m subplot, (3) mountain pine beetle tree baits in two flanking subplots, and (4) verbenone in the central subplot plus tree baits in flanking subplots, replicated seven times over 2 years. When verbenone was combined with tree baits, beetles were more consistently displaced from central subplots to the two flanking subplots than when verbenone was used alone.

L. Rasmussen (personal communication) tested the push-pull strategy in central Idaho using three treatments: (1) control, (2) verbenone only (100 bubble caps/ha), and (3) tree baits (5 baits/ha), randomly assigned to plots. He found that baits were highly effective in attracting beetles

and inducing them to infest trees in the baited plots. However, verbenone and control plots had similar levels of infestation. He concluded that the attractive baits alone would be just as effective as using both baits in stands scheduled for logging and verbenone in adjacent stands.

Individual Tree Protection

The protection of individual trees of high value, such as those around homes and administrative sites, has been a long-term goal of research with antiaggregation pheromones. The protection of individual trees injured by prescribed fires is another goal, since such trees, particularly in plantations, are of high value.

Borden and Lindgren (1988) assessed the effect of different application rates of verbenone on lodgepole pine tree baited with the attractive mountain pine beetle bait. Treatments were (1) attractive tree bait alone, (2) bait and one verbenone bubble cap, (3) bait plus verbenone bubble cap and four additional verbenone bubble caps attached on adjacent trees, and (4) bait plus a verbenone bubble cap and nine additional verbenone capsules on adjacent trees. They reported no differences among the application rates of verbenone, all of which reduced the attack density on baited trees, the percent of available trees within 10 m of the baited tree that were attacked (spill-over attacks), and the numbers of spillover trees. Notably, the verbenone reduced the average attack density on baited trees well below the 40 attacks/m² believed necessary to kill the tree. More spillover trees occurred with the highest verbenone rate than with the two lower rates. In addition, only two of the 10 baited trees treated with one verbenone bubble cap were attacked. Five of the 10 trees receiving the higher rates of verbenone, and all 10 baited trees receiving no verbenone were attacked.

Amman and Ryan (1994) established a study to protect individual fire-injured trees in Central Idaho. Lodgepole pines were heat treated by burning peat moss around 70 percent of the basal circumference to kill the cambium. Treatments applied were: (1) fire-injured control, (2) uninjured control, (3) two verbenone capsules on fire-injured tree and, (4) two verbenone capsules and two ipsdienol capsules on fire-injured tree replicated 20 times. Mountain pine beetle were attracted into the plots by placing tree baits on metal posts 3 to 5 m from treated trees. Control treatments contained more unattacked and mass attacked trees; pheromone treatments contained more unsuccessfully attacked trees. Ipsdienol did not increase the efficacy of verbenone alone in protecting trees.

Shore and others (1992) tested the multifunctional role of *exo*-brevicomin and the response of mountain pine beetle to combinations of *exo*-brevicomin and verbenone. Their treatments consisted of: (1) verbenone bubble cap, (2) *exo*-brevicomin released from Eppendorf tubes at a "low" rate of 0.5mg/day, (3) *exo*-brevicomin released at a "high" rate of 2.5mg/day, (4) verbenone plus *exo*-brevicomin low rate, (5) verbenone plus *exo*-brevicomin high rate, and (6) unbaited control. Treatments were replicated 28 times.

They found that *exo*-brevicomin at both release rates induced mountain pine beetle attacks. Verbenone significantly reduced mountain pine beetle response to *exo*-brevicomin to the level of the response to unbaited controls. Verbenone treated trees were attacked less often than control trees, but not significantly so. None of the verbenone treated trees were mass attacked.

Discussion

Aggregation Pheromones

Aggregation pheromones are in operational use in British Columbia. Additional research on the semiochemical complex of the mountain pine beetle is under way (G. Gries, Simon Fraser University, Burnaby, BC, Canada, personal communication). In particular, there is a need for more efficient synthetic pheromones for use in artificial traps for mass trapping and detection purposes.

Antiaggregation Pheromones

At this time, the use of antiaggregation pheromones on an operational basis cannot be recommended. The inconsistent results from year to year within and between areas, and between tree hosts of mountain pine beetle, point to the need for much additional research before antiaggregation pheromones can be used effectively. There are several possible explanations for the inconsistent results, ranging from inappropriate verbenone release devices to genetic selection of beetles.

1. Stand microclimate may change as infestations progress within a given stand. As trees are killed holes are created in the canopy, thus allowing pheromones to dissipate out of the stem zone and into the area above the canopy (Fares and others 1980; Schmitz and others 1989). Shea and others (1992) have an excellent discussion of this topic and how it may have affected their aerial tests. The same may apply to ground applications of bubble caps.

2. Weather factors, particularly temperature, may have contributed to failure of tests, particularly in ponderosa pine stands. High temperatures result in above-average elution rates, causing some bubble caps to expire before the end of beetle flight period; cool temperatures result in low elution.

3. In the failed Idaho tests, the release of verbenone from bubble caps was consistent with previous tests. The enantiomeric blend of verbenone in the bubble caps was found to be (–)–80 percent. This blend should not be a problem (Rasmussen 1974). Genetic change of mountain pine beetle related to infestation of small diameter trees (in which phloem is thin) after larger trees (in which phloem is thick) have been killed may contribute to selection of beetles that tend to ignore the verbenone signal. K. Hobson (USDA Forest Service, Logan, UT, personal communication) found a significant difference in response of mountain pine beetle to traps baited with aggregation pheromones and verbenone in old compared to new mountain pine beetle infestations in Central Idaho. Verbenone reduced

attraction of mountain pine beetle by 99 percent in new infestations and 89 percent in old infestations.

4. Large beetle populations may lead to the treatment being overwhelmed, since attacks are initiated on many trees simultaneously. The likelihood of additional beetles landing on previously attacked trees increases, leading to a higher probability of successful attacks (tree mortality).

5. Sparse beetle populations may lead to non-significant results, since untreated blocks must sustain some level of attack to provide adequate controls. In several experiments, control blocks sustained little or no mortality.

6. Photoisomerization of verbenone to chrysanthenone, a compound that the mountain pine beetle does not respond to, increases with exposure to light (Kostyk and others 1993). Photoisomerization occurs much faster in stands of open canopy than those having a closed canopy because of the greater light penetration, and was a particular problem in some aerial applications.

Current research is aimed at discovering compounds that send a stronger message to beetles as to the unsuitability of the host resource. Semiochemicals currently being tested include pheromones of competing species (interspecific competition), compounds from non-host trees (Dickens and others 1992), and repellant host compounds (Hayes and others in press). Research using verbenone alone has provided some encouraging evidence that the use of antiaggregation pheromones may have operational utility. The addition of other repellant semiochemicals may provide consistent results, allowing antiaggregation semiochemicals to be included in operational tools for mountain pine beetle management.

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Current Status of Research with the Spruce Beetle, *Dendroctonus rufipennis*

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Abstract—One of the most promising tools for reducing natural resource productivity losses due to spruce beetles (*Dendroctonus rufipennis* (Kirby) in Alaska involves the use of semiochemicals. Results of past research and development activities on spruce beetle semiochemicals suggest a high probability that successful management systems can be developed through an aggressive research and development effort. From 1988 to 1993, a cooperative project between Forest Health Management, USDA Forest Service, Alaska Region, and the Pacific Northwest Research Station was conducted to develop operational use strategies employing semiochemicals to manage spruce beetle populations. These management strategies were divided into those utilizing aggregation semiochemicals for trap out and diversion trapping of beetles, and the antiaggregation pheromone MCH formulated as beads and bubble caps to prevent or reduce infestation of stands and logging slash. Results to date have been inconclusive but the use of semiochemical mixes is promising if applications can be adapted for cold climates.

As with other areas of the United States, there is a variety of pests in Alaska that affect forest health. In terms of extent of damage, economic considerations, and annual tree mortality, the spruce beetle is the primary tree-killing insect in Alaska. In fact, the spruce beetle is the most significant mortality agent of mature spruce in the United States and Canada. Outbreaks of this beetle have caused extensive mortality from Alaska to Arizona and have occurred in every forest with spruce stands. Spruce beetle damage results in the loss of 235,833 m^3 annually.

Spruce beetle activity increased throughout Alaska during 1993 as on-going and new infestations covered approximately 257,470 ha (U.S. Department of Agriculture in press). The majority of these infestations are recent; however, the initial infestation started in 1972 in stands of white spruce near Hope in south-central Alaska. The first reported spruce beetle outbreak in Alaska occurred in 1922. It appears that after 70 years, the live residual

stand has again become susceptible to spruce beetle activity; scattered infestations have been occurring in this area for the past 15 years.

Preferred hosts of the spruce beetle are large diameter (20.3 cm), slowly growing white spruce (*Picea glauca* [Moench] Voss), Sitka spruce (*P. sitchensis* [Bong.] Carr.), and Lutz spruce (*P. x lutzii* Little) a hybrid of white and Sitka spruce (Werner and others 1977). Black spruce (*P. mariana* [Mill.] B.S.P.) is rarely attacked. Stands of Lutz spruce that have supported the majority of spruce beetle outbreaks are located in south-central Alaska, which has a transitional climate between maritime and continental conditions. The area is, therefore, more conducive to rapid population increases as generation times can be reduced from one generation every 2-3 years to one generation per year. Sitka spruce is less susceptible and suitable to attack than either white or Lutz spruce (Holsten and Werner 1990).

Management Strategies

Forest managers can develop various strategies to mitigate resource losses to spruce beetles. Currently, strategies used to reduce impacts of spruce beetles in Alaska involve some form of stand manipulation (Hard 1985, 1987, 1989; Hard and Holsten 1985; Werner 1978; Werner and others 1977) or treatment with approved insecticides (Werner and Holsten 1992; Werner and others 1983,1984, 1986a,b). Among the recommended techniques for treatment of logging slash, felled, or windthrown green trees is the immediate salvage of the trees (Werner and others 1977); or disposal by burning, chipping, or burying (Werner 1978). These techniques are short term but provide residual tree protection where potential problem areas are accessible and include high-value trees. Techniques are needed that reduce beetle-caused mortality in high-value areas until the stresses caused by competition or drought are alleviated. The most promising tools for reducing bark beetle losses in the short-term involve the use of behavioral chemicals such as semiochemicals. Semiochemicals are message-bearing chemicals that include insect-produced pheromones and host-produced volatiles that signal attraction or inhibition to the insects.

Beetle Manipulation Strategies

Trap Trees—Several control strategies were previously mentioned; however, these strategies are useful only where infestations are accessible, an uncommon occurrence in Alaska with little more than 4,800 km of road. If a small number of infested trees occur in an accessible area, then

unbaited trap trees, trap trees enhanced with semiochemicals, or sanitation thinning are effective strategies (Gray and others 1990). Trap trees are effective in attracting beetles up to 400 m. One trap tree is as effective as five to 10 standing trees. For infestations in inaccessible locations, baited trap trees are a viable option if the trees can be treated before beetle flight; otherwise, lethal trap trees are the only suppressive option if removal of trap trees is impractical.

Semiochemicals—The use of semiochemicals has several advantages: (1) ready access to treatment areas may not be necessary since aerial application of a semiochemical might be possible, (2) there would be no direct mortality to other parasites and predators as occurs with conventional insecticide treatments, and (3) the use of semiochemicals is more favorably received by the general public than traditional insecticide use.

The spruce beetle, like other species of bark beetles, produces aggregation and antiaggregation pheromones (Rudinsky 1973; Rudinsky and others 1974). When spruce beetles attack live standing trees, they attack quickly and in force to overcome the trees' defenses. If the beetles fail to overcome a host, the host successfully deters and usually kills attacking beetles with the production of oleoresin and other toxic secondary compounds (Werner and Illman 1994). Female spruce beetles, on encountering a suitable host for colonization, produce and release a powerful attractant that signals to other dispersing beetles of both sexes the availability of a suitable host. Mass attack and colonization quickly follow. When population densities of spruce beetles reach a critical level within a colonized tree, female spruce beetles produce an antiaggregation pheromone, 3-methylcyclohex-2-enone (MCH) (Rudinsky 1973; Rudinsky and others 1974) that signals to flying beetles that the host is occupied.

Beetle Management Strategies Using Semiochemicals

Results of research and development activities on bark beetle semiochemicals suggest a high probability that successful management systems can be developed through an aggressive research and development effort (Holsten in press). From 1988 to 1993, a cooperative project between Forest Health Management, U.S. Department of Agriculture, Forest Service, Alaska Region, Anchorage, AK, and the Institute of Northern Forestry, Pacific Northwest Research Station, U.S. Department of Agriculture, Forest Service, Fairbanks, AK, was dedicated to "The Development of Strategies for Spruce Beetle Management in Alaska Using Semiochemicals." This project had two phases:

Phase I: Development of new semiochemicals

   a. To develop and optimize pheromone blends for attracting spruce beetles to traps and baited trees.
   b. To determine the semiochemicals that deter spruce beetles from entering traps or from attacking trees.

   c. To determine the best release rates of the pheromone blends that are either attractive or repellent to spruce beetles.

Phase II: Operational use of semiochemicals

   a. To develop strategies for monitoring endemic spruce beetle populations using semiochemicals in traps and on trap trees.
   b. To develop strategies for effective beetle management using aggregation and antiaggregation semiochemicals.

Phase I from 1988 to 1991 included the development of an improved pheromone blend for attracting spruce beetles. This new blend was a ternary formulation that included α-pinene, frontalin, and 1-methylcyclohex-2-enol (MCOL) (Dixon and others 1992; Werner in press; Wieser and others 1991). This phase also included field tests using similar testing methodologies on the efficacy of the new blend in northern and southern Alberta, British Columbia, and south-central and interior Alaska. Phase II in 1992 to 1993 was proposed to demonstrate the efficacy of utilizing improved formulations of semiochemicals for manipulating spruce beetle populations in various management strategies.

Current Research

Beetle Management Strategies Tested in Alaska

Recently the use of semiochemicals to manipulate bark beetle populations has gained interest in Alaska (Holsten 1994; Werner in press). This includes aggregation and antiaggregation pheromones, host volatiles, or combinations to prevent attack or reduce the attack density of bark beetles to a level below the threshold density required for the development of brood trees.

Aggregation Semiochemicals—Field tests on the efficacy of various scolytid pheromones as attractants for the spruce beetle were done in Alaska in the late 1970's (Werner in press). A new ternary blend of spruce beetle lure (Wieser and others 1989) was tested in stands of white spruce in interior Alaska and Lutz spruce in south-central Alaska from 1988 to 1991. The efficacy of the ternary blend (frontalin release rate [RR] 0.1 mg/d, α-pinene RR 0.7 mg/d, MCOL RR 0.5 mg/d) was tested simultaneously against that of the binary blend of α-pinene and frontalin and proved superior by a wide margin; spruce beetles were attracted in greater numbers in all areas of the field test. The success of the efficacy trials led to field tests of various operational use strategies.

Antiaggregation Semiochemicals—The use of antiaggregation pheromones has the largest potential "payoff" of all operational use strategies in Alaska because it is more cost effective than other methods. The results of field tests on the efficacy of various formulations and dosages of MCH in Alaska are described in the next section.

MCH Field Tests—Field studies on the efficacy of slow-release formulations of MCH in liquid, granular, bead, and bubble caps were conducted between 1983 and 1993 in south-central Alaska (Holsten and Werner 1984, 1985, 1986, 1987; Werner in press). In 1983, liquid and granular formulations of MCH applied around felled trees at 9.2 and 13.8 kg/ha significantly reduced beetle attacks and beetle brood when compared to the untreated controls. Subsequent studies in 1984 and 1985 did not result in significant reductions in attack densities or brood production. Further studies in 1986 and 1987 suggested that the cool microenvironment of the forest floor and the undersides of felled trees was a major factor in preventing complete elution of the MCH from granules formulated to elute at 20 °C. A field test was conducted in 1987 to determine efficacy of MCH-impregnated bubble caps formulated to release MCH at 16 °C with an elution rate of 5 mg/day. Treatments reduced the number of attacks by 54 percent, but had no effect on number of egg galleries and progeny. Treatment did cause a reduction in length of egg galleries. In 1991, an aerial application of MCH applied at a rate of 4.6 and 9.2 kg/ha and a ground application at rates of 9.2 and 13.8 kg/ha were unsuccessful because of low beetle populations (Holsten and others 1992). There was insufficient beetle pressure on the untreated control plots to show a treatment effect. A field test was conducted in 1992 to determine the efficacy of MCH dispensed from bubble caps (400 mg of MCH; elution rate 3-4 mg/day at 24 °C) in protecting individual trees in a

campground. The MCH bubble cap treatment did not result in a significant reduction of successfully attacked trees. Spruce beetle pressure was extremely high in the study area and it was concluded that the naturally produced aggregation pheromone masked the MCH that eluted from the bubble caps.

In 1993, ground applied MCH beads at various dosage levels did not protect felled trees from beetle infestation in a powerline right-of-way (ROW) (table 1) (Werner in press). Plots were baited with pheromone since beetle pressure was light; however, pheromone baits were removed when control trees received attacks. In another study, 0.2-ha stands of beetle-infested Lutz spruce treated with MCH beads at 13.4 g/ha received no protection from attack by spruce beetles (table 2) (Werner in press). Bubble caps applied to standing trees in 1993 at a density of 77 and 120/ha protected 83 and 95 percent of the trees, compared to 79 percent of the trees in the control plots (table 3). These plots were not baited with spruce beetle aggregation pheromone because stands contained a high density of spruce beetles and beetle pressure was adequate.

The use of MCH bubble caps appears feasible as an operational use strategy for protecting high value stands of spruce where spruce beetle populations are low, but increasing. However, MCH does not elute sufficiently from MCH impregnated beads to deter spruce beetles in south-central Alaska. Soil surface temperatures on north aspects range from –1.0 to 10.0 °C from mid-May to mid-August; south aspect temperatures range from –0.5 to 9.9 °C. Ambient air temperatures 4 feet above ground level range from 2.2 to 28.0 °C on north aspects and 1.1 to 32.0 °C on south aspects. MCH beads are formulated to elute at 20 °C therefore, the lack of efficacy is probably related to the temperature of the microenvironment of the beads. The elution of MCH from beads needs further study in cold climates.

Interspecific Competition—Attracting competing bark beetles to suitable spruce beetle hosts may interfere with spruce beetle development and survival. Thomson and Sahota (1981) showed that competition effects on parent beetles during egg gallery establishment resulted in reduction in gallery length and oviposition. Safranyik and Linton (1985) demonstrated that density-dependent compensatory processes operate in spruce beetle populations during egg gallery construction and brood development when such populations compete for space. Whitmore

Table 1—Effect of MCH beads in reducing spruce beetle attacks in felled Sitka spruce on a powerline ROW, Seward, AK, 1993

Treatment beads	Competing species pheromone[1]	Average brood	Range
ha/kg		- - - - - - - - - -*No.*- - - - - - - -	
9.2		5.7b	3.1-12.0
13.4		2.6a	6.1-23.5
13.4+	Ipsdienol	9.9b	6.8-14.6
13.4+	Brevicomin mix	12.2a	6.1-24.5
Control		7.5b	3.8-14.1

[1]Racemic ipsdienol (0.2 mg/d), 50:50 brevicomin (3.8 mg/d).
[2]Means within columns followed by the same letter are not significantly different (*P* < 0.5, Tukey's [1953] Studentized Range [HSD] test).

Table 2—The effect of a ground application of MCH beads in reducing spruce beetle attacks in standing Lutz spruce, Falls Creek Road, AK, 1993

Treatment	Total trees	Unattacked trees	New 1993 Attacks	New 1993 Pitch outs	1992 attacks	Percent new attacks
			- -*No.*- -			
Beads[1]	174	45.7 ± 8.5a	7.3 ± 2.3a	0.8 ± 0.1a	3.3 ± 1b	13.8 ± 3.1b
Control[2]	64	41.0 ± 0.0a	1.0 ± 0.0a	4.0 ± 1.0a	19.0 ± 8a	0.4 ± 1.1a

[1]13.4 kg per ha. Values are the means from three 0.2-ha plots.
[2]Values are the means from one 0.2 ha plot. Values followed by the same letter are not significantly different (*P* < 0.5, Tukey's Studentized Range Test [HSD]).

Table 3—The effect of MCH bubble caps in reducing spruce beetle attacks in standing Lutz spruce, Falls Creek Road, AK, 1993

Treatment bcaps/ha	Total trees	New 1993		1992 attacks	Percent new attacks
		Attacks	Pitch outs		
		------ No. ------			
77	492	9.8 ± 2.2b	2.3 ± 0.4a	21.5 ± 4.8b	16.7 ± 3.6b
120	424	3.2 ± 1.0a	1.5 ± 0.5a	12.0 ± 2.5a	5.6 ± 1.4a
control	501	13.5 ± 2.9c	1.3 ± 0.2a	18.8 ± 3.3b	21.3 ± 4.3b

(1983) reported that the most important arthropod factor impacting populations of spruce beetles was interspecific competition with other species of scolytids. Whitmore (1983) also reported that small scolytid species were competing with spruce beetle in 73 percent of the bark samples (100 cm^2) in which spruce beetle were found. *Dryocoetes affaber* and *Polygraphus rufipennis* were the most important scolytid competitors found in felled spruce.

A study was initiated in 1991 to test the feasibility of using scolytid pheromones to increase interspecific competition with spruce beetles and thereby reduce spruce beetle brood production and survival in felled trap trees. A secondary objective was to determine if dispersing spruce beetles were repelled from an attractive source when they encountered pheromones from competing species. The study was done in stands of white and Lutz spruce and initially used baited Lindgren funnel traps in a completely randomized block design. The following pheromones were tested alone and in various combinations: the ternary blend from spruce beetles, a brevicomin mix of *endo:exo* from *D. affaber*, 2-methyl-3-buten-2-ol from *P. rufipennis*, and racemic ipsdienol from *I. perturbatus*. The addition of either methyl butenol or ipsdienol to spruce beetle pheromone reduced the catch of spruce beetles compared to spruce beetle pheromone alone (table 4) (Werner and Holsten in press). The combination of methyl butenol + brevicomin mix + ipsdienol added to the spruce beetle pheromone resulted in decreased spruce beetle catches compared with spruce beetle pheromone alone. The

combinations of the brevicomin mix + ipsdienol and the brevicomin mix + methyl butenol added to spruce beetle pheromone-baited traps caused the greatest reduction (86 percent) in spruce beetle catch.

The study continued in 1992 and compared number of spruce beetle attacks, gallery number and length, and brood development between felled green trees baited with spruce beetle pheromone and various combinations of (+)-ipsdienol, the brevicomin mix, and MCH. The study was conducted in two different areas, one with a low population and one with a high population. The addition of pheromones from competing species had little impact on spruce beetle attack and development in the high population area, except the addition of MCH was significant for gallery number, gallery length, parent adults, and brood larvae (table 5) (Werner and Holsten in press). There appeared to be significant reduction in attack density at the low population sites when the brevicomin mix and ipsdienol were added to the spruce beetle pheromone. There also was a significant reduction in attack density, gallery number, gallery length, and parent adults when MCH and the combinations of brevicomin mix + ipsdienol + MCH, brevicomin mix + MCH, and ipsdienol + MCH were added to the spruce beetle pheromone (table 5).

Trap Out—The use of semiochemicals to manipulate populations of spruce beetles using trap-out techniques was conducted in 1992 and 1993. The aim of the study was to pull beetles from infested stands into open areas

Table 4—Mean number of scolytids caught in funnel traps by various bark beetle pheromones alone and in combination, south-central Alaska, 1991

Treatment	Mean + SD			
	Spruce beetle	*Polygraphus*	*Dryocoetes*	*Ips*
SB pheromone	141.8 ± 223.8a	0.59 ± 1.32b	6.62 ± 36.2b	0.00 ± 0.00b
Methyl butenol (MB)	25.7 ± 37.7c	0.25 ± 0.67b	0.63 ± 1.8b	0.06 ± 0.25b
Brevicomin mix (BM)	1.7 ± 2.1e	1.16 ± 2.34b	16.00 ± 32.2a	0.03 ± 0.18b
Ipsdienol (IP)	24.6 ± 41.8c	1.28 ± 2.82a	1.28 ± 2.7b	0.25 ± 0.51b
SB X MB	55.8 ± 68.6b	1.06 ± 1.93b	1.25 ± 2.0b	0.31 ± 0.82b
SB X BM	28.5 ± 44.5c	3.00 ± 4.66a	21.00 ± 47.8a	0.03 ± 0.18b
SB X IP	94.2 ± 150.6b	0.47 ± 1.27b	3.44 ± 17.1b	17.97 ± 70.43a
SB X MB X BM	19.2 ± 25.0d	0.91 ± 1.25b	11.50 ± 25.1ab	0.00 ± 0.00b
SB X MB X IP	30.8 ± 60.8c	0.38 ± 0.75b	2.12 ± 4.4b	0.41 ± 0.91b
SB X BM X IP	17.9 ± 42.6d	0.44 ± 0.72b	13.84 ± 24.9ab	0.06 ± 0.25b
SB X MB X BM X IP	47.3 ± 75.2b	1.59 ± 3.35a	22.66 ± 53.8a	0.16 ± 0.57b
Control	6.7 ± 10.4e	0.38 ± 0.83b	0.16 ± 0.5b	0.03 ± 0.18b

Means within columns followed by the same letter are not significantly different ($P < 0.05$, Tukey's Studentized Range Test [HSD] [Tukey 1953]). SB = α-pinene + frontalin + MCOL; brevicomin mix = *endo:exo* brevicomin (50:50); IP = racemic ipsdienol.

Table 5—Comparison of semiochemicals that induce competition of other scolytids with spruce beetles in areas with high and low populations of spruce beetles

Treatment	Beetle attacks	Gallery number	Gallery length	Parent adults	Brood larvae	Brood pupae	Callow adults
High population							
Control	NS	NS	NS	NS	S	NS	NS
SB Pher	NS	NS	NS	NS	NS	NS	NS
SB+BM	NS	NS	NS	NS	NS	NS	NS
SB+BM+IP	NS	NS	NS	NS	S	NS	NS
SB+BM+IP+MCH	NS	S	NS	NS	S	NS	NS
SB+BM+MCH	NS	S	NS	NS	S	NS	NS
SB+IP	NS	NS	NS	NS	NS	NS	NS
SB+IP+MCH	NS	NS	NS	NS	NS	NS	NS
SB+MCH	NS	S	S	S	S	NS	NS
Low population							
control	NS	NS	NS	NS	NS	NS	NS
SB Pher	NS	NS	NS	NS	NS	NS	NS
SB+BM	S	NS	NS	NS	NS	NS	NS
SB+BM+IP	NS	NS	NS	NS	NS	NS	NS
SB+BM+IP+MCH	S	S	S	S	NS	NS	NS
SB+BM+MCH	S	S	S	S	NS	NS	NS
SB+IP	S	NS	S	NS	NS	NS	NS
SB+IP+MCH	S	S	S	S	NS	NS	NS
SB+MCH	S	S	S	S	NS	NS	NS

NS = no significant decrease, S = significant decrease ($P > 0.05$).
SB = α-pinene + frontalin + MCOL, BM = *endo:exo* brevicomin (50:50), IP = racemic ipsdienol, MCH = methylcyclohexenone.

or areas of nonhost type that contained pheromone-baited funnel traps. Plots consisted of 1.2- to 2.0-ha spruce stands with 15 to 35 percent of the trees infested with 1-and 2-year cycle beetles. Traps were placed in open areas such as road rights of way, treeless areas, or areas with nonhost types. This experiment ran 2 years to ensure 2-year cycle beetles were captured.

A minimum of 10 treated and 10 untreated control plots were used. Plots were selected that had four open or nonhost type areas in four different directions from and within 30 m of the infested plots. Four groups of five funnel traps (Lindgren[R] 12-funnel) were placed in the four open areas. Four traps were spaced at 3-m intervals with the fifth trap in the center of the square formed by the other four traps. One bait of the ternary formulation of α-pinene, frontalin, and MCOL (RR = 3.4 mg/d) was placed in the four corner traps and a bait containing 5 percent frontalin in the center trap. A buffer strip at least 90 m wide separated each

of the treatment and control plots. Traps were hung on L-shaped metal posts with the bottom of the collection container a minimum of 0.30 m from the ground. Beetles were trapped from June to August.

The number of successful attacks before and after treatment were compared between treated and control plots to evaluate the success of the trap-out technique. All spruce 7.6 cm DBH in an area 20 by 20 m in the center of the infested plot were evaluated in May before treatment and in early September after the first and second years of the study. Attack densities were estimated based on the lower 1.8 m of the trunk and were expressed as: no attack, light attack density (<10 attacks), medium attack density (10 to 25 attacks), and heavy attack density (>25 attacks).

The average number of spruce beetles caught from each of the 10 stands of spruce during 8 weeks of trapping was 173 (range 68-277). This number was rather low when compared to the amount of spruce beetle activity, as indicated by infested trees, in the area of the study. The number of new attacks in 1992 and 1993 and the percentage change between pretreatment and posttreatment attack densities are shown in table 6. Attack densities of 1-year beetles increased for both treated and control plots in 1992. Two-year beetle attacks decreased in the treatment plots by 28 percent in 1993; attacks in control plots increased by 62 percent (table 6).

Several factors could have contributed to low beetle catch: (1) the ternary spruce beetle pheromone was not effective in "pulling" beetles from the baited stands, (2) the baits were placed in the traps after beetle flight had started, (3) the baited stands had more trees infested with

Table 6—Effect of trap out on beetle-attacked trees

Treatment[1]	Number trees attacked[2]		Percent change
	Pretreatment	Posttreatment	
Pheromone			
1992	39 ± 7	50 ± 10	+34
1993	18 ± 3	13 ± 3	−28
Control			
1992	25 ± 5	49 ± 9	+49
1993	14 ± 2	37 ± 9	+62

[1]1992 = 1-year beetles, 1993 = 2-year beetles.
[2]Mean number ± SD.

2-year cycle beetles, (4) some of the baited traps were too far from the ground inventory plots, (5) additional spruce beetle baits may be needed, and (6) more baited traps may be needed around the infested stands.

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Applications of Semiochemicals in the Management of Southern Pine Beetle Infestations: Current Status of Research

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Abstract—The current status of semiochemical research for management of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), is summarized. Studies being conducted by the Texas Forest Service, the University of Georgia, and Virginia Polytechnic and State University involve application of semiochemicals to (1) suppress expanding beetle infestations, (2) change the direction of infestation spread, (3) protect individual high value pines, (4) document seasonal flight and response patterns, and (5) forecast beetle infestation trends. Synthetic verbenone, in a 34%(+):66%(−) enantiomeric ratio, has shown efficacy for halting infestation spread, for changing the direction of infestation spread (when combined with frontalin), and for protecting high value trees, including cavity trees of the endangered red-cockaded woodpecker, from beetle attack. The ultimate goal is to develop and implement various operational pest management tactics for the southern pine beetle.

In recent decades, the southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), has been the target of more intensive and frequent direct control programs in the United States than any other bark beetle species. Justification for periodic suppression activities throughout the southern United States, Mexico, and Central America rests on unique attributes of this scolytid pest. Among these are (1) a multivoltine life cycle with 3-12 overlapping generations per year and females capable of establishing multiple broods (Thatcher and others 1980); (2) a strong tendency to kill host trees in concentrated groups (spots) and ability to expand infestations rapidly from a few trees to hundreds of acres in the absence of intervention (Gara 1967; Hedden and Billings 1979); (3) capability to infest and kill pine hosts of all ages beyond 5 years of age as infestations expand, regardless of the tree's physiological condition (Lorio 1986; Thatcher and others 1980); (4) infestation cycles that reach peak levels every 6-9 years in certain portions of its range (Price and others 1992); and (5) availability of practical and cost-effective direct control methods that minimize potential resource losses (Billings 1980; Redmond and Nettleton 1990; Swain and Remion 1981).

In an effort to develop alternative means of managing outbreak populations of SPB, attention in recent years has focused on semiochemicals. The current status of research and experimental field applications of SPB semiochemicals is summarized below.

Suppression of SPB Infestations with Semiochemicals

Several beetle- and host-produced volatiles govern the host selection and mass attack behavior of the SPB (Payne 1980; Vité and Renwick 1968). The female-produced compound, frontalin, is the primary aggregation pheromone of SPB (Kinzer and others 1969). When combined with α-pinene or pine turpentine, synthetic frontalin has proven useful for inducing SPB attacks on standing trees (Vité and Francke 1976) or as a bait for use in trapping systems to monitor SPB populations and forecast SPB infestation trends (Billings 1988).

Inhibitory compounds produced by male SPB include verbenone (Payne 1980; Renwick 1967) and *endo*-brevicomin (Payne and others 1978; Silverstein and others 1968; Vité and Renwick 1971). Verbenone is a major component of the pheromonal blend emitted by male SPB and a minor component of that emitted by females (Pitman and others 1969). At low concentrations, (S)-verbenone released by females enhances the response of males to the attractive blend of frontalin, *trans*-verbenol, and α-pinene (Rudinsky 1973; Rudinsky and others 1974). Males, after arriving on attacked trees, begin releasing verbenone at much greater rates than the females. The increasing levels of verbenone and other inhibitory compounds reduce further attraction of males to the tree (Renwick and Vité 1969, 1970). At high concentrations, other flying beetles, both males and females, shift their destination to the next available pine (Gara 1967).

Of the semiochemicals isolated from SPB, verbenone has received the most attention as a potential SPB control tactic. In early field tests, Payne and Billings (1989) demonstrated that (S)-verbenone applied to freshly-attacked trees and uninfested pines around the leading edge of

small expanding SPB spots slowed rates of spot growth. A more effective treatment for completely disrupting the growth of SPB infestations consisted of felling all freshly-attacked trees in combination with applying (S)-verbenone to nearby uninfested (buffer) trees. Although these tactics showed promise, the authors recognized the need for additional replications and modifications in the deployment of verbenone before the tactics could become operational. The following summarizes the current status of programs to develop semiochemical-based suppression and manipulation tactics for the southern pine beetle. Emphasis is placed on progress made since 1989. For a review of earlier work, see Payne 1980; Payne and Billings 1989; Payne and others 1992; and Vité and Francke 1976.

Enantiomeric Ratios and Elution Devices

Payne and Billings (1989) reported that *D. frontalis* produced verbenone at an enantiomeric ratio of 15%(+):85%(−). Field tests have shown that both racemic and (S)-verbenone are effective inhibitors for SPB (Payne and Billings 1989; Payne and others 1978). More recently, field bioassays with attractant-laden traps (Salom and others 1992) demonstrated that an enantiomeric ratio of 34%(+):66%(−) verbenone was more inhibitory to adult SPB than the (S)-verbenone used in previous treatments to suppress SPB infestations (Payne and Billings 1989). The former was therefore used as the inhibitory component for both suppression and manipulation treatments described here. Methods for deploying verbenone under field conditions have evolved over the years. Payne and Billings (1989) applied verbenone in a liquid polymer mix sprayed onto portions of target trees. The polymer solidified on the bark surface, eluting verbenone over a 40 to 50 day period. Inconsistencies in the composition and availability of the polymer carrier, however, led to further research into alternative elution devices.

In 1989 studies, 17%(+):83%(−) verbenone was deployed from sponges sealed within 5- by 10-cm clear, 1.0 mil polyethylene bags. Two of these devices, each containing 4 ml of verbenone, were attached to each target tree; the verbenone eluted through the sealed bag at a rate of approximately 80 mg/day for a period of 45 to 50 days. These devices worked well under moderate field temperatures (15 to 25 °C). Under high temperatures (>30 °C), the verbenone within these bags was found to convert to chrysanthenone, losing its inhibitory properties (Ted Shaver, personal communication). This shortcoming was eventually overcome through further experimentation. A white 0.75-1.0 mil thick polyethylene bag filled with 5 ml of verbenone was determined through field and laboratory biossays to be superior to thicker bags or those made from gray, brown, or black polyethylene (Salom and others 1992). The sealed white bag (5- by 10-cm) eluted verbenone at rates averaging 9.4 mg/hour for 20 to 30 days during summer months (Salom and others 1992).

For 1993 studies, this bag was replaced with an 8 by 13 cm white polyethylene bag of 1.2 mil thickness, provided by Phero Tech, Inc., Delta, BC. The Phero Tech bag provided an elution rate of 9.2 mg/hr for 40 to 50 days during summer months (C. W. Berisford, personal communication). The 34%(+):66%(−) verbenone used in 1990-1993

studies was formulated by mixing two parts 17%(+):83%(−) verbenone (Bedoukian Research, Danbury, CN) with one part 69%(+):31%(−) verbenone (Phero Tech Inc., Delta, BC).

Evaluation Methodology for Semiochemical Suppression Tactics

Among potential applications of semiochemicals that have been proposed for suppressing individual southern pine beetle infestations, two tactics have received the greatest attention in recent years. Both involve use of synthetic verbenone in a 34%(+):66%(−) enantiomeric ratio deployed from 0.75 to 1.2 mil white polyethylene bags. In 1990 to 1993, the efficacy of verbenone only and verbenone combined with tree felling for suppressing SPB infestations was evaluated in replicated field trials in several southern States. A third treatment, consisting of felling all infested trees only, was applied to additional spots to ascertain the extent to which tree felling as such contributes to suppression. For each treatment, efficacy was measured by (1) comparing pretreatment rates of spot growth (trees killed per day) with rates of spot growth during a 6-week post-treatment period, and (2) comparing post-treatment rates of spot growth to those predicted to occur by the Arkansas spot growth model (Stephen and Lih 1985) in the absence of treatment. Each year and within each region of the South where verbenone was evaluated, model predictions were checked against untreated infestations to validate model performance (Billings and Upton 1993).

Verbenone Only—This tactic consists of applying two or three bags of verbenone to pines undergoing attack and uninfested buffer trees in a 10-m strip around the leading edge of expanding infestations as described previously (Billings and Upton 1993; Payne and Billings 1989). From 200 to 1,000 ml of verbenone are applied per spot, depending on the size of the infestation and the average tree diameter. As a rule of thumb, as many trees are treated with verbenone as there are currently-infested trees in a given spot. Tests of the "verbenone only" tactic using the same experimental procedures were conducted from 1990 to 1993 in Georgia (15 spots), Alabama (10 spots), Virginia (10 spots), Texas (7 spots), and North Carolina (1 spot).

Verbenone + Tree Felling—This tactic involves a combination of verbenone applied to standing, uninfested buffer trees located within 10 m of the advancing head of the spot and the felling of infested trees that would contribute to infestation expansion. Tree felling may involve only trees undergoing attacks by adult beetles (Payne and Billings 1989) or all freshly-attacked plus currently-infested trees in the spot (Billings and Upton 1993). The former treatment is aimed solely at eliminating sustained production of beetle-produced attractants within the treated spot; the latter mimics a conventional cut-and-leave treatment (without felling uninfested buffer trees) that also serves to open up the stand, may increase mortality to developing broods, and promote interspecific competition among bark-inhabiting insects within felled brood trees. Treatment efficacy also may be increased because beetles emerge in drastically changed environmental conditions (stand openings) that we believe are more

conducive to dispersal than to aggregation. The procedure of verbenone plus felling freshly-attacked trees has been tested in Texas (7 spots) using polymer spray formulations of (S)-verbenone (Payne and Billings 1989). More recently, the same tactic has been tested using 34%(+): 66%(−) verbenone deployed from white polyethylene bags on three spots in Texas, two in Georgia, and one in Alabama. The treatment involving verbenone and felling all infested trees has been tested only in Texas (26 spots), using 34%(+): 66%(−) verbenone.

Felling All Infested Trees Only—Eleven infestations (10 in Texas and one in Georgia) was treated by felling all infested trees only, without felling uninfested (buffer) trees or applying verbenone. Mean reduction in rates of spot growth resulting from this treatment was compared to that produced by the combination of verbenone plus felling all infested trees.

Efficacy of Suppression Tactics

Results of all field evaluations conducted from 1990 to 1993 are listed in table 1. Verbenone only, tested on a total of 43 spots in five southern states, reduced post-treatment spot growth by an average of 61 percent, compared to pre-treatment growth rates. With the exception of the single spot treated in North Carolina, mean growth rates were reduced most (69 percent) for spots in Texas and least (55 percent) for spots in Georgia. On average, beetle populations in 44 percent of the treated spots expanded beyond the treated buffer. The greatest proportion of verbenone-treated spots that exceeded the buffer occurred in Texas where average tree size was considerably larger than that of trees on spots in Alabama, Georgia, and Virginia. By contrast, only one of 10 spots expanded beyond the verbenone buffer in Alabama, where average tree diameters and average numbers of infested trees per spot were smaller.

The "verbenone plus felling freshly attacked trees only" treatment was evaluated on six spots in three different states, with mixed results. The method completely halted spot growth within the treated buffer on two of three spots in Texas and one spot in Alabama. For reasons that remain unclear, this tactic failed to even slow rates of spot growth the two times it was tried in Georgia in 1991. Earlier tests of this tactic conducted in Texas using a polymer spray formulation of (S)-verbenone revealed that spot growth was reduced by 87 percent and six of seven treated spots were effectively controlled (Payne and Billings 1989).

The "verbenone plus felling all infested trees" treatment was evaluated on 26 spots treated over a 3-year period in Texas. Spot growth rates were reduced by 90 percent, and 21 of the spots (81 percent) were completely halted within the treated buffer. Of all the semiochemical treatments evaluated to date to suppress SPB infestations, this combination has proven the most effective. Tests of this treatment in other southern States are currently being tested.

The partial treatment that involved felling all infested trees with no verbenone (check) provided additional evidence supporting the use of verbenone. Of 11 spots treated in Texas and Georgia from 1990 to 1992, seven continued to expand. Percent spot growth reduction for all 11 spots combined averaged 58 percent, compared to 90 percent for the same treatment plus verbenone.

Results of treatment efficacy described above and in table 1 were further confirmed for each treated spot by comparing post-treatment spot growth rates with those predicted to occur in the absence of treatment, using the Arkansas spot growth model (see Billings and Upton 1993; Payne and Billings 1989). Spots that were predicted to expand during the pretreatment monitoring period but not during the 6-week post-treatment interval were excluded from the analysis in table 1. In turn, post-treatment model predictions for 45 spots representing three

Table 1—Summary of treatments utilizing 34(+):66(−) verbenone, with and without tree felling, for suppression of southern pine beetle infestations; 1990 to 1993

Treatment	State	Year	Mean No. of infestations	D.b.h. (cm)	Mean Infested trees/spot(range)	Mean trees killed/day Before	After	Percent growth reduction	Percent of spots with trees killed beyond buffer
Verbenone only	TX	1990-92	7	23.4	61.0 (34-105)	1.79	0.56	69	71
	AL	1992-93	10	16.5	28.8 (13- 39)	1.07	0.37	65	10
	GA	1991-92	15	20.6	49.2 (14-198)	1.55	0.70	55	47
	VA	1992-93	10	20.0	66.4 (41-117)	2.78	1.09	61	60
	NC	1991	1	28.4	33	0.90	0.00	100	0
	Total		43	20.1	50.0 (13-198)	1.75	0.67	61	44
Verbenone + fell fresh attacks only	TX	1990-91	3	34.7	57.3 (31- 80)	1.14	0.43	62	33
	GA	1991	2	25.7	66.5 (60- 73)	1.00	2.30	−130	100
	AL	1993	1	42.4	34.0	1.38	0.12	91	0
	Total		6	33.0	56.4 (31- 80)	1.13	1.00	12	50
Verbenone + fell all active trees	TX	1990-93	26	29.9	68.5 (25-172)	2.52	0.24	90	19
Fell all active trees	TX	1990-92	10	26.9	92.9 (28-184)	2.30	0.99	57	60
	GA	1991	1	17.3	24.0 1.00	0.25	75	100	
	Total		11	26.0	86.6 (24-184)	2.18	0.92	58	64

different treatments conducted in Virginia and Texas were generated (fig. 1). Post-treatment model predictions were adjusted for each group of spots based on discrepancies between model predictions and actual mean spot growth values observed prior to treatment. Compared to post-treatment predictions, actual growth rates were reduced by 63 percent for verbenone only applied in Texas, by 56 percent for verbenone only applied in Virginia, by 90 percent for felling all infested trees plus verbenone in Texas, and by 59 percent for felling all infested trees without verbenone in Texas (fig. 1).

Other combinations of inhibitory and attractive semio-chemicals are currently being tested by the Texas Forest Service. These include frontalin and rapidly-released host volatiles (Billings 1985) applied to brood trees with and without felling pines with fresh attacks, verbenone plus green leaf volatiles (Dickens and others 1992), and verbenone buffer plus baiting brood trees with frontalin and rapidly-released host volatiles. Although there have been insufficient replications of these variations to draw firm conclusions, to date none appears to be as effective for disrupting spot growth as verbenone and felling all infested trees.

Manipulation of SPB Infestations with Semiochemicals

There is need for a method to manipulate SPB infest-ations, not necessarily for purposes of suppression, but simply to change the predominate direction of spread. Such a strategy would be particularly useful in wilderness areas to protect adjacent private lands, or to preserve ha-bitat or colony sites of the endangered red-cockaded wood-pecker (RCW). The potential of using semiochemicals for changing the direction of SPB infestation spread was evaluated in East Texas, using two different methods.

Evaluation Methodology for Semiochemical Manipulation Tactics

In tests conducted during 1991 and 1992, a verbenone buffer was established as described for the "verbenone only" suppression treatment. Simultaneously, to induce attacks on uninfested pines for purposes of spot manipu-lation, one Eppendorf capsule in a brown polyethylene pouch was attached to each uninfested target pine. The capsule contained 400 micrograms of 99 percent pure frontalin, provided by Phero Tech, Inc. The number of trees baited with attractant was equal to the number of trees undergoing attack at the time of treatment. The at-tractant lures were attached with a staple gun, one per tree, at a height of 2 m. Spots were monitored for 1 week prior to treatment to confirm the rate and direction of spot growth, then for 4 weeks post-treatment. The num-ber and d.b.h. of trees attacked by SPB at each weekly in-terval, together with their location within the treated spot (original head or baited head), were recorded. The ma-nipulation was considered successful if beetle attacks in the treated infestation shifted from the original head to
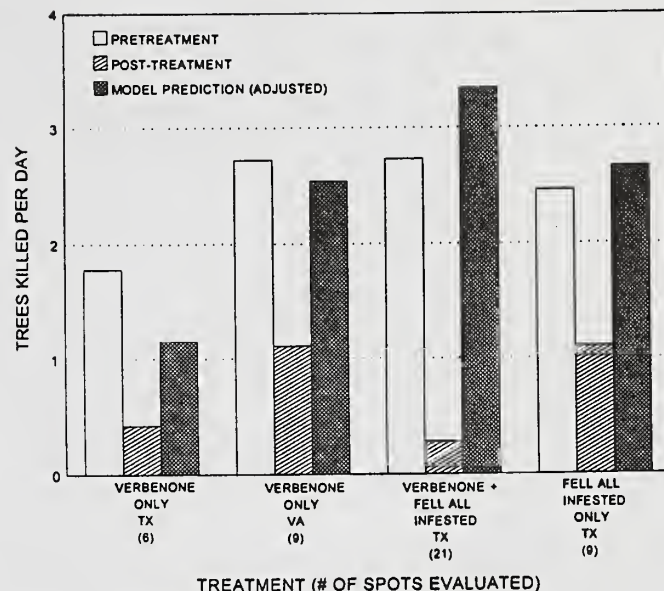

Figure 1—Mean numbers of new trees killed per day during pre- and post-treatment intervals compared to post-treatment predictions pro-duced by the Arkansas spot growth model for southern pine beetle infestations treated in Virginia and Texas with verbenone only, in Texas with verbenone plus felling all infested trees, and in Texas with felling all infested trees without verbenone 1990 to 1993.

the baited head during the 4-week post-treatment obser-vation period. Seven infestations, ranging in size from 25 to 85 infested trees, were treated.

A second procedure aimed at changing the direction of spot spread involved baiting small infestations (13 to 44 active trees) solely with frontalin. For every tree under-going attack within each of three spots, two uninfested trees were baited with frontalin as described above, with-out use of verbenone at the original head. Pre- and post-treatment monitoring procedures were the same as de-scribed above.

Efficacy of Manipulation Tactics

Results (table 2) showed that SPB populations emerg-ing within moderate-sized infestations can be directed to infest preselected host trees with application of verbenone and frontalin placed strategically within the spot. In all seven treated spots, the predominate direction of infesta-tion spread was reversed within 1 to 3 weeks following ap-plication of semiochemicals. After 1 to 4 weeks, all fresh attacks were in the vicinity of the baited portion of treated spots, providing evidence of successful manipulation.

Similar results were obtained using frontalin only for three small-sized infestations treated in East Texas in 1993 (table 2). Whether manipulation of larger infestations can be successfully achieved without use of verbenone re-mains to be demonstrated.

Table 2—Summary of numbers of additional trees attacked per week at the original baited heads within SPB infestations manipulated with verbenone plus frontalin (V+F) or frontalin only (F only); East Texas 1990-1993

Year	Treatment mo/day	Spot (#)	Treatment	No. of Infested trees	Ml. of verbenone	Trees w/frontalin	Mean d.b.h. (cm)	Head	Week with respect to treatment date				
									−1	+1	+2	+3	+4
1990	8/17	038A	V+F	41	150	6	30	Original	[1]10	5	1	0	0
								Baited	0	16	9	4	12
	8/24	038B	V+F	54	250	5	33	Original	9	9	2	9	5
								Baited	0	14	8	3	9
1991	7/30	1053	V+F	62	480	10	30	Original	20	2	6	0	0
								Baited	0	10	4	1	6
	9/04	1334	V+F	25	250	10	36	Original	10	0	2	0	0
								Baited	0	3	8	4	1
	9/05	1332	V+F	81	620	14	25	Original	14	7	1	0	0
								Baited	0	28	10	25	5
1992	7/23	2417	V+F	73	320	10	28	Original	20	6	1	0	0
								Baited	0	9	4	6	1
	9/14	2675	V+F	85	460	10	20	Original	20	23	10	3	0
								Baited	0	4	18	2	1
	9/28	2692	V+F	55	450	15	20	Original	16	1	1	0	0
								Baited	0	15	5	8	2
	9/28	2693	V+F	77	500	15	33	Original	18	2	0	0	0
								Baited	0	11	5	8	7
1993	6/23	3185	F only	44	0	11	31	Original	11	1	3	0	[2]
								Baited	0	5	22	3	[2]
	7/09	3291	F only	15	0	4	43	Original	2	0	0	0	0
								Baited	0	6	3	1	1
	7/07	3316	F only	13	0	4	36	Original	2	2	0	0	0
								Baited	0	9	0	0	1

[1]Number of additional trees attacked per week.
[2]Spot controlled before monitoring period was completed.

Protecting Individual High-Value Pines from SPB Colonization

Field experiments are being conducted to evaluate the efficacy of synthetic verbenone for preventing the initial attack and subsequent colonization of high value pines by the southern pine beetle. Of particular value would be the capability to protect cavity trees of the red-cockaded woodpecker (RCW). Living pine trees that serve as required nesting sites for this endangered species are subject to frequent SPB attacks and high levels of mortality, particularly during the SPB's fall dispersal period (Conner and others 1991).

Methodology for Protecting Individual Pines with Semiochemicals

In 1992, 70 RCW cavity trees in East Texas were treated with verbenone in late October or early November. An equal number of nearby cavity trees in the same RCW colonies were randomly selected as paired check trees (no verbenone treatment). Both verbenone-treated and check trees were monitored at periodic intervals until May 1993 to record SPB attacks.

In addition, 28 RCW cavity trees were detected within 1 week after the initiation of attacks by SPB during October 1992. Fifteen of these trees were treated immediately with verbenone while the remainder were left untreated. Treated and untreated trees were monitored periodically for 8 months. The proportion of treated and untreated pines that survived SPB attack was recorded. For individual tree protection experiments, verbenone was applied at levels of 3, 6, and 10 m above the ground. At each level, one 0.85 mil white polyethylene bag and one 2.5 mil white polyethylene bag, each containing 10 ml of 34%(+):66%(−) verbenone, were attached with staples to two sides of the tree bole (60 ml verbenone per tree).

Efficacy of Single Tree Applications of Semiochemicals

By the end of January 1993, four of the 70 check trees had been attacked by SPB; three were subsequently killed. None of the verbenone-treated cavity trees was attacked prior to February 1993. One verbenone treated tree was attacked and killed after January 1993, presumably because the verbenone had dissipated from the elution devices after 3 months of exposure. These studies are being repeated in Texas and Louisiana in 1993 and 1994.

Of 15 RCW cavity trees treated within 1 week of the initiation of SPB attacks, only five (33 percent) were subsequently killed, compared to 11 of 13 untreated RCW cavity trees (85 percent). It is very uncommon for southern pines to resist SPB colonization, once initial attacks have begun.

In related studies, researchers at the U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station in Pineville, LA, are evaluating 4-allylanisole, a component of loblolly pine oleoresin, for protecting individual pines from SPB attack. Results from laboratory and field tests have been promising (Hayes and others 1994).

Other uses of SPB Semiochemicals

Multiple funnel barrier traps (Lindgren 1983), baited with frontalin and rapid-release dispensers of loblolly pine turpentine (Billings 1985), were monitored at weekly intervals throughout the year for several consecutive years in East Texas. Results from these studies serve to document the seasonal abundance and distribution of SPB as they disperse in search of new hosts outside established infestations. As shown in figure 2, SPB adults are commonly trapped outside established infestations throughout the year in East Texas. Maximum trap catches consistently occur during the spring (March to May), presumably representing the period of long-distance dispersal. Following dispersal, beetles initiate most multiple-tree infestations (expanding spots) during this season—the same infestations that are detected by aerial survey in peak numbers during June, July, and August (fig. 2).
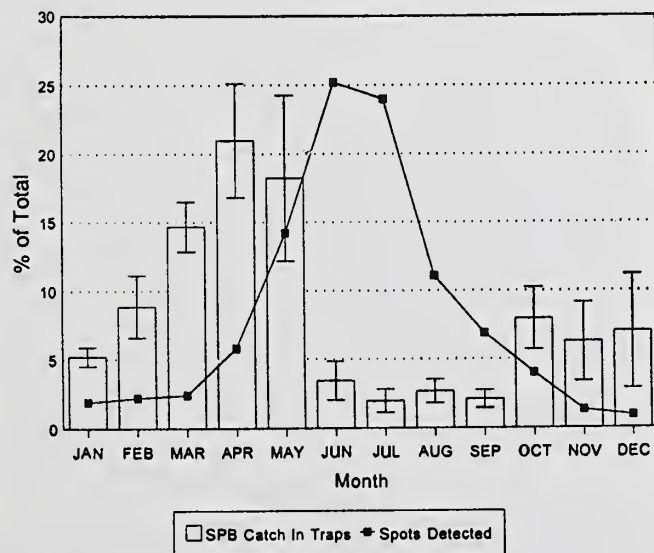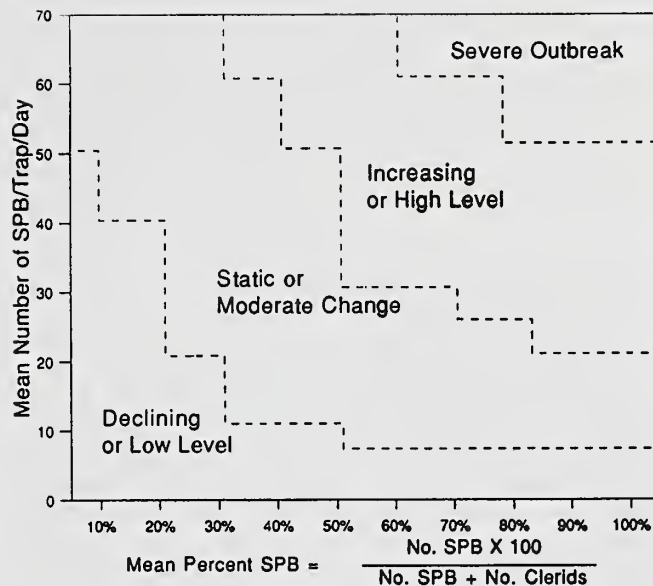
Figure 3—Chart for forecasting southern pine beetle infestation trends for the current year in the southern United States, based on early season responses of *Dendroctonus frontalis* and the clerid *Thanasimus dubius* in frontalin and turpentine-baited Lindgren funnel traps (modified from Billings 1988).

Emerging beetles remain concentrated in established infestations throughout the summer months, attacking trees on the periphery of the same infestation in which they developed, in response to continual production of aggregation pheromones (Gara 1967; Hedden and Billings 1979). Adult SPB disperse to a lesser extent again during the fall (October and November). The predator *Thanasimus dubius* (F.) (Coleoptera: Cleridae) shows a distinct synchrony with its preferred host, *Dendroctonus frontalis*. Most clerids in East Texas are trapped in the fall, winter, and spring (October to April) outside infestations, with the fewest during hot summer months (R. F. Billings, unpublished data).

In recent years, the Texas Forest Service has developed and implemented a practical system for forecasting SPB infestation trends. The procedure uses Lindgren barrier traps baited with frontalin and rapid-release dispensers of pine turpentine (Billings 1988). Three traps per county or Ranger District are monitored weekly for a 4-week interval during the principal SPB dispersal period, which occurs in March, April, or May, depending on geographical location. The mean number of SPB per trap per day and the ratio of SPB to clerid predators (*Thanasimus dubius*), expressed as percent SPB, are correlated with subsequent infestation trends (increasing, static or declining) for the current year. Trap catches are averaged for a given county or Ranger District and plotted on a modified prediction chart (fig. 3) to forecast SPB infestation trends. With cooperation from numerous State, Federal, and university cooperators, this forecast system has been implemented annually since 1986 in some 60 locations within 11

Figure 2—Seasonal patterns of southern pine beetle response to pheromone-baited traps (percent of mean total catch per year and standard error) and aerial detection of new multiple-tree infestations in Tyler County, TX, from 1986 to 1990.

southern States (Texas, Arkansas, Louisiana, Mississippi, Alabama, Georgia, Tennessee, Virginia, North Carolina, South Carolina, and Maryland). Since becoming operational, the system has correctly predicted infestation trends in 70 to 80 percent of the counties or National Forest Ranger Districts surveyed (R. F. Billings, unpublished data).

Discussion and Plans

Suppression strategies and tactics used to address SPB outbreaks have changed over the years. The early strategy of beetle population reduction, applied from 1950 to 1970, relied extensively on chemical insecticides. Due to high costs, dubious effectiveness, and adverse side effects, this *brute force* approach aimed at eliminating the beetle has been replaced with one of damage avoidance. Current pest management programs are based on improved knowledge of SPB biology and seasonal behavior (Branham and Thatcher 1985; Thatcher and others 1980). Individual multiple-tree infestations are now detected by periodic aerial surveys (Billings and Ward 1984), evaluated for spread potential (Billings and Pase 1979a; Stephen and Lih 1985), and assigned a control priority. Those having a potential to cause excessive timber losses are targeted for prompt suppression, using mechanical tactics (Billings 1980; Swain and Remion 1981).

All currently infested trees, plus a 10 to 30 meter buffer of uninfested trees at the leading edge of the spot, are felled and harvested (cut-and-remove) or left on site (cut-and-leave). When applied to infestations with 20 to 100 currently-infested trees in the Gulf Coastal region, the cut-and-leave method (Billings 1980) halts further spot expansion, particularly during hot summer months. In the southern part of the beetle's range, this treatment disrupts the SPB attack process by terminating the production of beetle- and host-produced attractants and eliminating those hosts most likely to be colonized by pheromone-induced aggregation (Vité and Renwick 1968). During summer months, beetles that survive increased solar radiation and interspecific competition in felled trees are forced to disperse under conditions of high temperatures and increased host resistance (Lorio 1986).

Beetle infestations treated with salvage or cut-and-leave seldom exceed 0.5 ha in size, untreated infestations have commonly killed all available hosts over hundreds, and occasionally thousands of hectares. The principal disadvantage of cut-and-leave is that this tactic requires the felling of numerous uninfested trees to assure spot disruption, a sacrifice many landowners are reluctant to make. In addition, cut-and-leave has not proven as effective as a suppression tactic in the northern portions of the beetle's range, where SPB produce fewer generations per year and attack behavior is not as seasonally dependent.

Field tests conducted in various southern States have demonstrated that SPB semiochemicals show considerable promise for suppressing infestation growth. At 10 ml per tree, 34%(+):66%(–) verbenone was relatively effective in slowing down infestation growth, particularly for spots containing fewer than 50 infested trees of pulpwood size

(less than 20 cm d.b.h.). The most effective treatment developed to date involves felling all infested trees and applying verbenone to uninfested buffer trees at the leading edge of the infestation. At least in Texas, the combination of verbenone and felling all infested trees is more effective than verbenone alone for completely disrupting infestation growth, particularly for large infestations and those in sawtimber-sized stands. Further testing, however, is needed on SPB infestations outside Texas.

As with cut-and-leave, felling trees serves to interrupt the natural production of beetle- and host-produced attractants that govern spot growth processes. Once levels of natural attractants within the infestation are reduced by tree felling, the verbenone is more likely to protect adjacent uninfested trees. Also, in contrast to spots treated with verbenone only, beetle progeny emerging from previously-infested trees that have been felled are more likely to disperse out of the site, due to the drastically changed stand conditions. Evidence for this conclusion is provided by those spots treated with felling only; this partial treatment reduced infestation growth by an average of 58 percent (compared to 61 percent reduction for the "verbenone only" treatment).

Furthermore, the fact that the combination treatment of verbenone and felling all infested trees closely mimics cut-and-leave (a tactic widely used in Texas and other Gulf Coastal states since 1970) supports its eventual use as an operational SPB control tactic in this region. The disruption of expanding SPB infestations with cut-and-leave during summer months effectively reduces potential timber losses (Redmond and Nettleton 1990), without increasing the frequency of new spots (Billings and Pase 1979a,b; Fitzgerald and others 1994). Presumably, beetles have difficulties re-initiating multiple-tree, expanding infestations, once the spring dispersal phase has terminated (fig. 2). One would expect the same effect if verbenone were combined with tree felling on a large-scale basis, although not necessarily in the northern portion of the beetle's range or in the case of verbenone applied in the absence of tree felling. Whether beetles departing from a treated spot with unchanged stand conditions will tend to initiate new infestations nearby, particularly in regions with cooler ambient temperatures, remains to be determined.

The ultimate goal of current studies is to develop practical, effective, and environmentally sound methods to reduce resource losses from the SPB. Operational applications of synthetic verbenone must await registration of this semiochemical by the U.S. Environmental Protection Agency and commercial production of verbenone-filled elution devices, followed by technology transfer efforts to train potential users. Meanwhile, studies are continuing at the University of Georgia (UGA), Virginia Polytechnic Institute and State University (VPI and SU), and by the Texas Forest Service (TFS) to further evaluate the efficacy of various semiochemical-based suppression tactics. Also, scientists at the UGA will continue to test elution devices and elution rates of verbenone under a variety of laboratory and field conditions.

In related studies, researchers at VPI and SU carried out surveys on eight SPB spots from 1991 to 1993 to evaluate the influence of inhibitor-based suppression tactics

on population distribution of SPB natural enemies. Data from infestations where the verbenone only tactic was successful, unsuccessful, and was not applied (check) will be used to compare population and diversity parameters among the SPB and its more common insect natural enemies. Data from this project are currently being summarized and analyzed.

There is evidence that responses of SPB to its semiochemicals may vary depending on geographical region (Berisford and Payne 1988). Accordingly, experiments were begun in 1993 at VPI and SU to further document the extent to which SPB response to verbenone and other pheromones varies regionally throughout the South. Data have been collected in three SPB spots within each of three States (VA, SC, and TX). Replicated field bioassays utilizing pheromone—baited traps were used to evaluate the response of SPB to different pheromone blends in each State. Pheromone and host odors released from SPB-infested logs were collected to ascertain whether the composition of verbenone and α-pinene are related and if they vary among States. Data from this study are under evaluation (Grosman, D. M.; Salom, S. M.; Ravlin, F. W., personal communication).

The Texas Forest Service plans to further develop practical, biologically sound, and cost-effective tactics utilizing verbenone, frontalin, and/or green leaf volatiles (Dickens and others 1992) as a means to suppress or manipulate SPB infestations in Texas as well as to protect high value trees from SPB attack.

Once sufficient efficacy data, practical elution devices, and EPA registration are obtained, project personnel will initiate a technology transfer program to implement these new approaches to SPB management.

Acknowledgments

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Protection of a Rare Stand of Torrey Pine
from *Ips paraconfusus*

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Abstract—From 1989 through 1992 Torrey pine (*Pinus torreyana* Parry ex. Carr.) were being killed at exceedingly high rates in Torrey Pine State Reserve, California. The primary mortality agent was identified as *Ips paraconfusus* Lanier, the California fivespined ips. After considering several intervention options that included insecticides application, limited salvage logging, and watering, it was decided to attempt to suppress the Torrey pine mortality with a semiochemical-based management strategy. Both aggregation and antiaggregation pheromones of *Ips paraconfusus* were strategically deployed throughout the Reserve in Lindgren funnel traps to trap enough beetles to reduce Torrey pine mortality. After several seasons of pheromone-mediated trapping, mortality caused by *Ips paraconfusus* was virtually eliminated.

The Torrey pine (*Pinus torreyana* Parry ex. Carr.) is a beautiful and comparatively delicate conifer species with a life span of only about 200 years (Ledig and Conkle 1983). Mature Torrey pine have rounded open crowns with many large branches; needles occur in bundles of five (Hickman 1993). Torrey pines occur naturally only along the La Jolla-Del Mar coastal bluffs and on Santa Rosa Island in southern California. Once widely distributed along the Southern California coast into northern Baja California, Mexico, this very rare pine exists on the North American continent as an intact forest ecosystem only at Torrey Pine State Reserve. The approximately 48-hectare stand lies within the larger 700-hectare state reserve boundary administered by the California Department of Parks and Recreation. In the late 1800's this unique resource only numbered several hundred trees (Ledig and Conkle 1983); by 1991 there were approximately 7,000 trees in the stand.

The Reserve lies within a sprawling urban setting that is bounded on the west by the Pacific Ocean, the north by the city of Del Mar, the east by the City of San Diego, and the south by the city of La Jolla. The Torrey pine stand in the reserve is analogous to an oceanic island; the stand is located within a sea of scrub/chaparral vegetation type. The nearest stand of Torrey pine is 160+ kilometers distant on Santa Rosa Island off the coast of Los Angeles. The closest ornamentally planted Torrey pine is 3 to 5 kilometers south of the Reserve. The soil type is classified as coastal sandstone. Climatic conditions are often described as persistently droughty.

Torrey Pine State Reserve is a very popular day park; over 1.25 million people visit every year. The busiest days occur between mid-February and late May when the multitude of spring flowers are blooming. In addition to being considered a local treasure, with a nonprofit association dedicated to the preservation of Torrey pines, people from all over the world visit the park each year. Recreationists use the park for picnicking, hiking, bicycling, nature walks, beach access, and swimming. The two most popular trails are the Parry Grove and Guy Fleming Trails (each named after prominent botanists that worked in the Reserve in the early 1900's) that traverse the oceanside portion of the Torrey pine stand.

The Problem

By the winter of 1991 Reserve officials and patrons had observed hundreds of Torrey pines dying within the Reserve, the vast majority within the Guy Fleming and Parry Grove trail systems. The mortality was determined to have been caused by *Ips paraconfusus* Lanier, the California fivespined ips. Discussions with Reserve personnel and others provided evidence for the following course of events. During December 1988 there was a fierce winter storm that resulted in about 25 trees being blown down throughout the Reserve. This blowdown was quickly colonized by the endemic population of *I. paraconfusus*. The first unusual amount of Torrey pine mortality was not reported until late summer of 1989. The previous history of insect activity in the Reserve had been limited to an occasional isolated Torrey pine or small group (1 to 3 trees) being killed by *I. paraconfusus*.

During the spring and summer of 1990 tree mortality continued to increase and by the fall of 1990, group kills of 20 to 30 trees each were observed throughout both the Guy Fleming and Parry Grove trail systems and along the Razor Point trail in the southern portion of the Reserve. By the winter of 1991 virtually 100 percent of the Torrey pines located between the Pacific Ocean and the main access road, located about 300 meters upslope from the ocean, had been killed by *I. paraconfusus*.

Reserve managers considered several unattractive intervention options to reduce or eliminate the escalating tree mortality. Application of insecticides for treating currently infested trees, killing developing broods, and protecting uninfested trees from new attacks was rejected as too toxic and indiscriminate. Watering the Torrey pines in hopes of strengthening their defense systems against

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attack was considered not feasible for so large a stand. Thinning the stand with a limited logging operation was unacceptable not only from an esthetic standpoint but also because of the probable damage that would occur to the many species of sensitive plants in the Reserve.

It must also be emphasized that between 1988 and 1993 California experienced a severe drought that further exacerbated the problem. When evaluating the situation during the winter of 1991 it was concluded, given the circumstances of many newly infested trees and continued drought, that the infestation would proceed if left unmanaged. This would result in many additional Torrey pines being killed.

The Insect

The California fivespined ips (CFSI), *I. paraconfusus*, a native of the United States, is limited in distribution mainly to California along the west side of the Sierra Nevada mountains. Although beetles prefer downed material (trees or portions of trees lying on the ground due to wind, logging, or snow breakage) this species is capable of killing saplings and pole or sawtimber size trees and has been recovered from most species of pines within its range of distribution. Attacks on live trees are usually limited to trees suppressed or stressed by dwarf mistletoe, root disease, drought, fire, or attack of other insects (Furniss and Carolin 1977).

Attack by CFSI is initiated by males that bore a nuptial chamber in the inner bark. The male then releases an aggregation pheromone that attracts other insects, both male and female, to the attack site. If many beetles are attracted to a specific site, excess beetles may "spill over" and successfully attack nearby trees, causing a group-kill. In addition, most bark beetles also produce an anti-aggregation pheromone that inhibits a continuous arrival of beetles to a single tree. These compounds have the effect of regulating the negative effects of intraspecific competition by reducing overcrowding that may result in lowered brood survival (Borden 1985). Within a day or two of the initial attack by the male, two to five females will enter the nuptial chamber for mating. After mating, each female constructs an egg gallery by boring through the phloem between the xylem (sapwood) and the cambium (Birch 1978; Furniss and Carolin 1977).

The size and shape of the combined gallery patterns are often diagnostic for the species of *Ips* involved. The CFSI gallery pattern resembles a tuning fork. The galleries are kept clean or open by beetles pushing boring dust out the entrance hole. This reddish colored boring dust collects in bark crevices or on spider webs and is evidence of a successful attack. Eggs are laid along the sides of the galleries. When larvae hatch they begin feeding on the phloem. Larvae eventually pupate in cells at the end of the larval mines and after 7 to 10 days moult to the callow adult state (Furniss and Carolin 1977).

A generation time of 6 to 8 weeks, from egg to adult, is typical for spring populations of CFSI (Furniss and Carolin 1977). Generation time during the summer is usually reduced to about 4 to 6 weeks. It is not unusual to have several overlapping generations occurring at one location during the summer. Depending on winter temperatures, the beetles may cease development and overwinter in any of the life stages. In the San Diego area it appears that brood development, although slowed considerably, continues throughout the winter months.

The aggregation pheromones of CFSI, the first bark beetle pheromone to be fully described, consist of the following three compounds: (–) ipsenol, (+) cis verbenol, and (+) ipsdienol (Silverstein and others 1966). The antiaggregation compound used for the CFSI consists of the aggregation compound of the potential competitor, *I. pini*, (–) ipsdienol (Light and Birch 1979). Recent research has shown that some pheromones have interspecific effects in addition to intraspecific effects. Paine and Hanlon (1991) have shown that the addition of (–)-verbenone, the antiaggregation compound for many *Dendroctonus* species, may enhance the inhibitory effect of (–) ipsdienol on CFSI. Given this information it was decided that an operational scale pheromone based management strategy would be attempted to reduce or eliminate the anticipated Torrey pine mortality caused by CFSI.

The Strategy

It is necessary to emphasize that the information reported in the remainder of this paper is not the result of an experiment and as such is limited in its validity to imply cause and effect. This project was undertaken as an operational demonstration and a "last ditch" effort to lower the rate of Torrey pine tree mortality. The primary object was to remove enough beetles through the employment of pheromone-baited Lindgren funnel traps (Lindgren 1983) and antiaggregation pheromones to impact the amount of Torrey pine mortality occurring within the Reserve.

The strategy employed is commonly referred to as "trap-out" and has been used on varying scales with varying results (Bakke 1991; Wood 1980). The strategy has many variations that include trap trees (baited and unbaited), toxic trap trees, and baited traps of various configurations, all of which have the basic objective of concentrating large numbers of beetles and removing or killing them. It is assumed that by removing a large number of beetles tree mortality will be reduced, but this strategy has never been rigorously tested with well-designed field experiments.

As previously stated the Reserve's stand of Torrey pine mimics an "island"; no Torrey pines or any other pines occur within 3 to 5 kilometers. It can be assumed that most, if not all, of the CFSI beetles attracted to baited funnel traps are within the stand boundaries.

Beginning in May 1991, 10 sets of three black Lindgren funnel traps were strategically placed every 20 to 80 meters apart in a line approximately 270 meters long. Traps were hung on dead Torrey pines approximately 30 meters inside the dead portion of the stand and parallel to the green uninfested stand. The use of dead trees for trap placement was considered necessary because: (1) of the need to reduce the risk of killing any additional trees as a result of possible "spill-over" (Wood 1980); (2) there is evidence that some beetles require a suitable silhouette to be attracted to baited funnel traps (Tilden 1976; Wood 1980). This trap configuration resulted in a string of traps extending

from the middle of the Guy Fleming Trail system and proceeding south, ending in the southern portion of the Parry Grove Trail system. The constant presence of a westerly breeze off the Pacific Ocean was an added advantage since it carried the pheromone plume from the traps toward any emerging beetles and thereby pulled them away from the green uninfested stand.

The traps were baited with CFSI commercially available pheromones (Phero Tech, Inc.) formulated in a controlled release bubble cap device. The specific pheromones used were: (+)50%/(−)50% ipsenol ([−]-2-methyl-6-methylene-7-octen-4-ol; (+) cis-verbenol (cis-4,6,6-trimethyl-bicyclo [3.1.1] hept-3-en-2-ol); (+)97%/-%3% ipsdienol ([+]-2-methyl-6-methylene-2,7-octadien-4-ol). These pheromones were formulated to last approximately 75 days.

In addition to the aggregation pheromones, 10 sets of two antiaggregation pheromones, also contained in bubble caps, were placed approximately 30 meters into the green uninfested stand and parallel to the funnel trap line. The antiaggregation pheromones were: (−)86%/(+)14% verbenone (4,6,6-trimethyl-bicyclo [3.1.1] hept-3-en-2-one) and (+)50%/(−)50% ipsdienol. Each antiaggregation compound was formulated in separate bubble caps to last approximately 70 days. Specific loading and release rates for all the pheromones are listed below:

Aggregation Pheromones

Ipsenol (+/−) 40-mg bubble cap, rr=0.2mg/day @ 24 °C
cis-verbenol 150-mg bubble cap, rr=0.3mg/day @ 24 °C
Ipsdienol [(+)97%/(−)3%] 40-mg bubble cap, rr=0.2mg/day @ 24 °C

Antiaggregation Pheromones

Verbenone [(−)86%/(+)14%] 790-mg bubble cap, rr=10 mg/day @ 24 °C
Ipsdienol (+/−) 40-mg bubble cap, rr=0.2mg/day @ 24 °C

During the initial trapping period, Reserve staff visited the traps weekly and placed the contents in zip-lock bags for storage in a freezer. During the last trapping period, the traps were visited on an irregular basis as stated in the results section. The collected beetles were shipped monthly to the bark beetle research facility in Placerville, CA. All scolytids and the most numerous predators were identified and counted. Voucher specimens were pinned and are presently maintained in the bark beetle collection in Placerville, CA.

Prior to the first trapping period (May 1991), the entire Reserve was surveyed to census the number of currently infested and dead Torrey pines. For each subsequent trapping period only currently infested trees were censused. The currently infested trees, which were detectable by the presence of pitch tubes and/or boring dust, were marked with a spot of paint. In addition the location of each currently infested tree for each trapping period was placed on a map for future reference.

Results and Discussion

The results of the mortality census taken in early May 1991 indicated that about 12 percent of the Torrey pine stand had been killed by CFSI during late winter of 1988 through May of 1991. This amounted to over 840 trees,

the vast majority of which were distributed within and between the Guy Fleming and Parry Grove trail systems. In addition, the census identified 38 trees that were currently infested with CFSI; all of these were located in the area between the green uninfested stand and currently dead area. These trees ranged in color from lime green to slightly yellow and contained CFSI life stages ranging from early larvae to callow adults.

Over 330,000 CFSI beetles were removed by pheromone trapping from Torrey Pine State Reserve during three time periods extending from May 1991 to September 1993. In 1991 a total of 156,520 CFSI were trapped between May 15 and October 24. Average trap catches ranged from a high of about 1,000 beetles/trap/week during Week 4 (June 15, 1991) to a low of less than one beetle/trap/week during Week 18 (October 24, 1991) (fig. 1). Actual numbers of CFSI ranged from a high of 29,000+ to a low of 25 beetles for the same time periods mentioned previously. The number of predators (only *Temnochila chloridia* were recovered from the Lindgren funnel traps) caught in the traps during 1991 showed a much different flight pattern than CFSI. Early in the season low numbers of predators/trap/week were caught compared to later in the season (<1/trap during Week 4 vs. >4/trap during Week 14). The total number of predators removed during the first trapping period was 669, which resulted in a ratio of predators to CFSI of 0.004.

After the week of October 24, 1991, the pheromone baited Lindgren funnel traps were removed from the Reserve. This decision was made because only two additional trees were infested by CFSI during the trapping period May to October 1991. These trees were first noticed in mid-August of 1991. It seemed reasonable to remove the traps for several reasons. The numbers of beetles being caught had decreased to very low levels and many individual traps were empty. Additionally, there were at least 38 currently infested trees at the beginning of the trapping period in mid-May and only two additional trees had become infested by October of the same year. This period spanned 19 weeks. If 6 to 8 weeks is considered the normal generation time for CFSI we should have seen
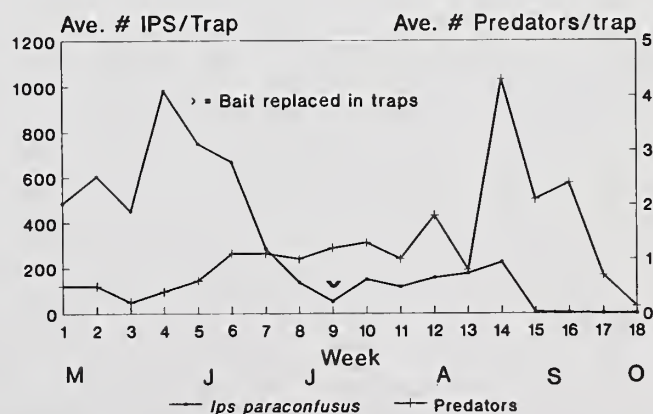

Figure 1—Average trap catch of *Ips paraconfusus* and associated predators of Torrey Pine State Reserve, 1991.

several periods of mortality. There was no evidence of this within the time period discussed.

In late January 1992 Reserve personnel reported the presence of several fading trees within the Guy Fleming trail system. A few weeks subsequent to this a thorough census discovered 14 trees currently infested with CFSI. The pheromone-baited Lindgren funnel traps were redeployed in mid-March 1992 in the same configuration as previously described. This second trapping effort lasted 36 weeks, starting the week of March 18, and continuing until the week of December 17. In excess of 158,000 CFSI beetles were removed from the Reserve during this time.

The total number of beetles trapped during the 1991 and 1992 seasons was very similar but average monthly trap catches were very different. In 1991 monthly trap catches averaged 26,086 beetles/month compared to 15,814 beetles/month in 1992 (table 1). In addition the 1992 weekly average never reached the level experienced in 1991 (figs. 1, 2). The flight periodicity of beetles in 1992 also was quite different than in 1992. As indicated by the peak in figure 1, there was an initial flight of beetles early in 1991 followed by a gradual decline in average weekly trap catches for the remainder of the trapping period (fig. 1). In contrast, the 1992 pattern showed two distinct peaks, one in April and another in August (fig. 2). Further, if you consider that the trap catches during week 14 of 1992 are misleading because the pheromones have been left unchanged for 98 + days and therefore are not attractive, there could easily have been an additional peak between week 13 and
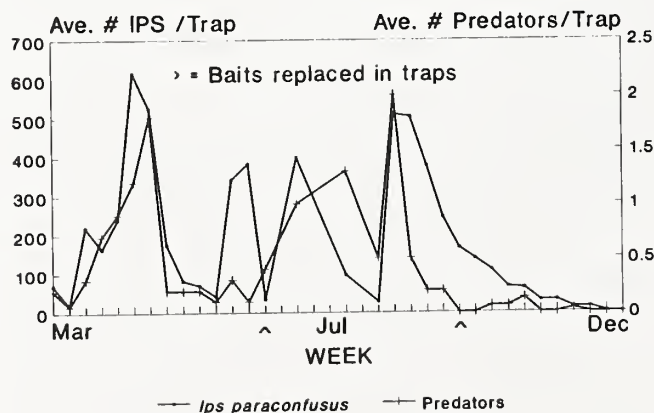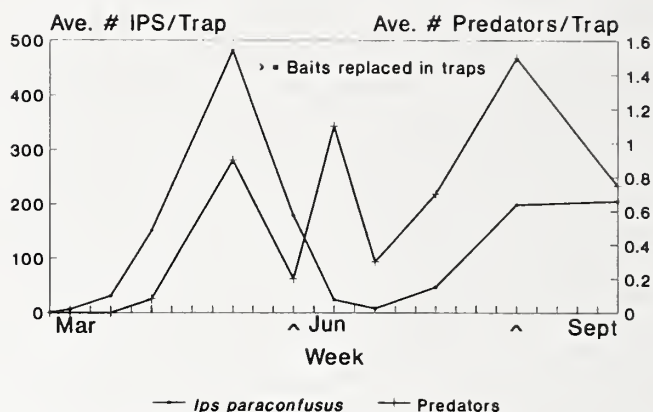

Figure 3—Average trap catch of *Ips paraconfusus* and associated predators at Torrey Pine State Reserve, 1993.

week 15 (fig. 2). Interestingly these peaks (including the imaginary week 14 peak) coincide closely to generation times of approximately 6 to 9 weeks.

In addition to lower average per trap catches of CFSI for 1992 compared to those in 1991, the average per week trap catches of predators was also lower (figs. 1, 2). Average per week trap catches of predators in 1992 never exceeded two predators/week; in contrast 1991 weekly catches exceeded four predators/week/trap. Also in contrast, the 1991 flight pattern of predators did not seem to track that of the CFSI, but in 1992 the predator flight pattern closely tracked that of the prey. There was approximately a 50 percent reduction in the total number of predators captured in 1992 vs. 1991 (334 vs. 669) even though the period of trapping in 1992 was twice that of 1991 (36 vs. 18 weeks).

Trapping in 1992 ceased after the week of December 17 because California Department of Parks and Recreation budget problems would not allow additional purchase of pheromones. Continuous monitoring of additional mortality from the original 14 Torrey pine trees found the previous January revealed that two additional trees were killed by CFSI during July of 1992. These two trees were located within the Guy Fleming trail system.

In March 1993 additional pheromones were purchased and a reduced trapping effort was resumed. Twelve traps, located at four sites (three traps per site) within the Guy Fleming trail system, were deployed during the week of March 17. Trapping was continuous over a 32-week period starting in mid-March and ending in late September. Traps were visited on an irregular basis varying from 1 to 4 weeks in length (fig. 3). During this trapping period 16,051 CFSI beetles were removed from the Reserve. Approximately 90 percent fewer beetles were caught (75 percent reduction when based on a per trap basis) in 1993 compared to 1991 and 1992. Total numbers of predators captured also decreased in 1993 (69 total predators) compared to 1991 and 1992 (table 1).

To this date (November 1993) no additional Torrey pine mortality has occurred within the Reserve boundaries since August 1992.

Table 1—Seasonal trap catches of *Ips paraconfusus* and associated predators (PREDS) at Torrey Pine State Reserve, 1991 to 1993

Year	Weeks	Total number CFSI (PREDS)	Average monthly catch
1991	18	156,520 (669)	26,086
1992	36	158,146 (344)	15,814
1993	32	16,051 (69)	2,293

Figure 2—Average trap catch of *Ips paraconfusus* and associated predators at Torrey Pine State Reserve, 1992.

Conclusions and the Future

It is not possible, with any degree of statistical certainty, to ascribe the swift and dramatic reduction in Torrey pine tree mortality to the pheromone trapping program. The very nature of the project did not lend itself to randomly assigned controls (there were none) or other amenities associated with controlled experimentation. Therefore we must evaluate the project using wholly subjective criteria. This is not totally dissimilar to other efforts to employ a pheromone based trap-out strategy (Bakke 1991). However, there are some notable differences between the trap-out project conducted at Torrey Pine State Preserve and previous efforts (Bakke 1991; Wood 1990). In the case of the Torrey Pine State Reserve the tree and insect populations were relatively small and neither were part of an extensive coniferous landscape that could harbor additional populations of CFSI. The Reserve is an ideally isolated "island" that was exceedingly conducive to employment of a pheromone based trap-out strategy. The overwhelming majority of beetles were always in close proximity to the baited traps. The pheromone plumes emanating from these traps were continuously carried by the constant and consistent westerly breeze toward the potentially susceptible beetles. The common problem of unwanted, spill-over mortality associated with baited traps was alleviated by hanging the traps in dead trees.

It seems more than mere coincidence that, when the pheromone trapping was discontinued in the early winter of 1991, new CFSI-caused Torrey pine mortality appeared within several months. It further stretches coincidence that this mortality should cease after the pheromone trapping was resumed in 1992. It is essential to point out also that during 1991 and 1992 California was in the midst of a very severe drought that should have enhanced the ability of CFSI to successfully attack standing live trees. Finally, when all factors are taken into consideration it is difficult to avoid concluding that the pheromone based trap-out program played a major, if not the only, role in the virtual elimination of CFSI as the primary cause of tree mortality in Torrey Pine State Reserve.

There have been many discussions with Reserve personnel concerning what management actions must be taken to prevent future CFSI infestations. All Reserve personnel need training on the identification of CFSI-caused tree mortality. Through this training the establishment of an ongoing monitoring system can be instituted so that future infestations will be recognized before they become serious problems.

The Torrey pine stand at the Reserve is a unique genetic resource and because of its genetic homogeneity is particularly vulnerable to stressful or catastrophic events. It is imperative that every reasonable effort be made to preserve this rare, beautiful, and scenic resource.

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Prospects of New Semiochemicals and Technologies

Gerhard Gries

Abstract—In 1966 to 1967 Silverstein and collaborators developed an elaborate six element protocol for insect pheromone research, and identified the first bark beetle pheromones. Employing the same or modified protocols, many coleopteran semiochemicals have been identified. However, there is contention that even species already studied have semiochemicals yet to be disclosed. Arn and collaborators in 1975 invented a coupled gas chromatographic-electroantennographic detector (GC-EAD) system that revolutionized moth pheromone research, and awaits intensive application for scolytid and curculionid beetles. As outlined in three examples, application of this most sensitive analytical tool, use of suitable logs for beetle colonization and pheromone production and proper treatment of beetles for GC-EAD and behavioural bioassays facilitate and/or expedite the identification of novel semiochemicals.

In 1967, Silverstein and collaborators published a standard protocol for the isolation and identification of new semiochemicals. This protocol comprises (1) development of a laboratory bioassay; (2) production of starting materials; (3) bioassay-monitored isolation of active components; (4) identification of active compounds by spectrometry and spectroscopy; (5) synthesis of putative structures and spectrometric (scopic) comparison of synthetic and natural compounds; (6) laboratory and field bioassays of synthetic compounds to confirm bioactivity.

Applying this protocol, Silverstein and others (1966) identified the first bark beetle aggregation pheromones for the California fivespined ips, *Ips paraconfusus* Lanier. While Silverstein's protocols remains the fundamental basis for (bark beetle) pheromone research, recent identification processes appear more expeditious. Airborne volatiles, possibly from single beetles (Birgersson and Bergstrom 1988; Gries and others 1988), are captured on Porapak Q (Rudinsky and others 1973), desorbed with solvents and subjected to gas chromatography (GC). Differential diagnosis (Vité and Renwick 1970) of male- and female-produced volatiles identifies the sex-specific volatile(s). Analysis of these candidate pheromones by coupled GC-mass spectrometry (Rudinsky and others 1973) is followed by assignment of putative structures and rational syntheses. Identical mass spectrometric and retention characteristics of synthetic and beetle-produced compounds confirm structural assignments and lead to laboratory and/or field bioassays of candidate pheromones.

Differential diagnosis allows identification of semiochemicals which are readily detectable by the flame ionization detector (FID) of the GC. Non- or hardly FID-detectable compounds remain unidentified and are extremely difficult to pinpoint even in conventional bioassays of extract fractions. Moreover, identification of host tree kairomones in Porapak Q extracts requires time consuming and labor intensive extract fractionations with subsequent bioassays to demonstrate behavioral activity of fractions or individual volatiles therein.

Innovative coupled gas chromatographic-electroantennographic detection (GC-EAD) (Arn and others 1975), with volatiles being simultaneously detected by the FID and an insect antenna (EAD), has expedited semiochemical identification in scolytid beetles, but requires careful selection of suitable trees (bolts) and use of well treated beetles.

Suitable Trees and Insects

In centuries past European foresters felled trap trees in the fall preceding spring bark beetle flight. Aging of trap trees over winter apparently changed their volatile composition and made them particularly attractive to host seeking pioneer beetles. Colonization of aged but not freshly felled trap trees with subsequent semiochemical-based mass attack, suggested that (optimal) pheromone production requires specific host conditions. Greater pheromone production of spruce beetles, *Dendroctonus rufipennis* (Kirby), when caged on naturally overwintered rather than freshly felled spruce, *Picea* spp., bolts (Gries and Gries, unpublished) substantiate the contention that production of starting material (bark beetle frass) for pheromone analysis requires careful selection of proper host plant material.

Use only of well treated beetles for pheromone production and analysis (GC-EAD and laboratory assays) is the second important criterion for semiochemical identification. Improper ambient conditions, particularly relative humidity and temperature, before, during and after beetle emergence may adversely affect the beetles' ability to produce and/or respond to semiochemicals. Lack of behavioral response of pedestrian beetles in laboratory bioassay at days of low atmospheric pressure (Members of the Chemical Ecology Research Group at SFU, unpublished) is consistent with the observation that beetles emerge and disperse in the forest at suitable meteorological conditions. Cold storage ($\leq$6 °C) of emergent beetles before use, as

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commonly reported, adversely affected pheromone production of *Ips latidens* (LeConte) (D. R. Miller, Phero Tech, Inc., unpublished data) and phenylalanine metabolism in *Ips pini* (Say) (Gries, unpublished data). Air cargo shipped, cold-exposed tropical weevils were commonly of lower quality for semiochemical analysis than weevils that were "carried on" by the visiting collaborator(s) (Gries and Gries, unpublished).

Coupled Gas Chromatographic-Electroantennographic Detection (GC-EAD) for Semiochemical Analyses of Scolytid and Curculionid Beetles

Arn and others (1975) invented a coupled gas chromatographic-electroantennographic detector system for moth pheromone research. Waddams (1984) demonstrated the applicability of this technique for bark beetle semiochemical research and even conducted GC-single cell recordings with antennae of the elm bark beetle, *Scolytus multistriatus* (Marsham). Despite their analytical potential, GC-EADs have rarely been employed in coleopteran semiochemical research. The following examples will demonstrate the efficacy of GC-EADs for the identification of candidate pheromones and kairomones and for the determination of pheromone chirality in scolytid and curculionid beetles.

Example 1: Candidate Semiochemicals in *D. rufipennis*

Although several aggregation pheromones including frontalin (Gries and others 1988), seudenol (Vité and others 1972), 1-methyl-2-cyclohexen-1-ol (MCOL) (Wieser and others 1992) and verbenone (Gries and others 1992) have been identified in *D. rufipennis*, there is evidence for additional as yet unknown pheromones. Subjecting extracts of female *D. rufipennis* frass (boring crumbs plus fecal pellets) to GC-EAD analyses revealed several antennally active compounds which are not accounted for by any of the known semiochemicals (fig. 1). These hardly FID-detectable, EAD-active compounds have been identified and are currently tested in field experiments.

Example 2: Kairomone Identification in African Oil Palm, *Elaeis quineensis* (Jacq).

Attraction of the African palm weevil, *Rhynchophorus phoenicis* L., to traps baited with synthetic aggregation pheromone (phoenicol) required the presence of synergistic oil palm tissue (Gries and others 1993). For analyses of oil palm kairomones, airborne volatiles of 1- to 4-day-old cut oil palm tissue were captured on Porapak Q, and Porapak Q extracts subjected to GC-EAD analyses (fig. 2). Of several EAD-active esters, ethyl propionate significantly enhanced pheromonal attraction in field experiments (Gries and others 1994).
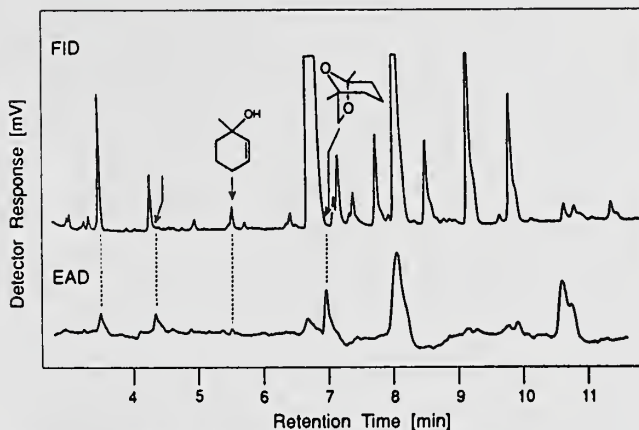

Figure 1—Flame ionization (FID) and male *D. rufipennis* antenna (EAD) responses to female *D. rufipennis* frass volatiles chromatographed on a DB-5-coated, fused silica column (1 min at 50 °C, 4 °C/min to 120 °C, then 20 °C/min to 240 °C).

Because GC-EAD analyses allowed rapid identification of candidate oil palm kairomones for tropical weevils, we have adopted the technology for analyses of bark beetle kairomones. Employing male or female fir engravers,
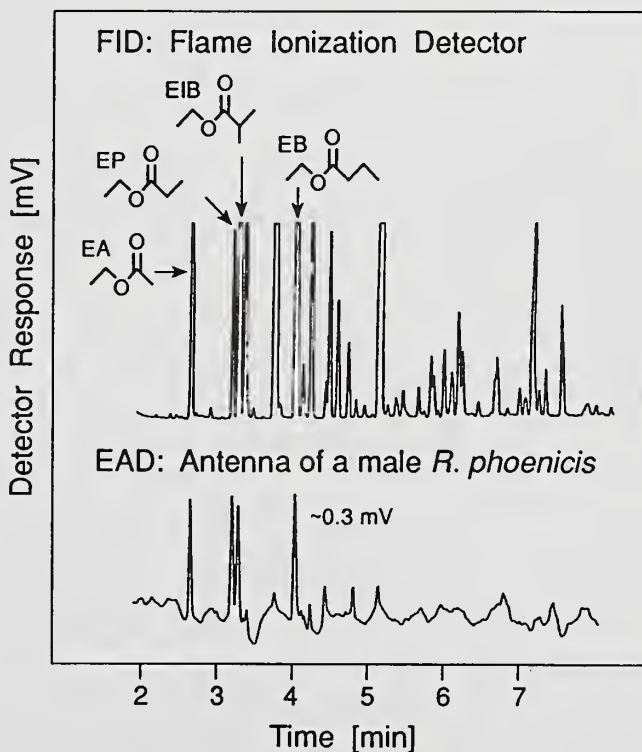

Figure 2—FID and male *R. phoenicis* antenna (EAD) reponses to African oil palm volatiles chromatographed on a SP-1000-coated, fused silica column (1 min at 50 °C, 10 °C/min to 180 °C) (adapted from Gries and others 1994).

Scolytus ventralis (LeConte), in GC-EAD volatile analyses of grand fir, *Abies grandis,* we obtained several antennal responses to quantitatively minor volatile components. These EAD-active compounds have been identified and are currently field tested for behavioral activity.

Example 3: Chirality Determination of *R. phoenicis* Aggregation Pheromone (Phoenicol)

The presence of non-beetle-produced enantiomers in synthetic pheromones may interfere with optimal attraction (Leal and Mochizuki 1993; Tumlinson and others 1977, Vité and others 1985). Determination of beetle-produced enantiomer(s) and/or stereoisomers is therefore required to fully elucidate the chemical communication system for a target species, and to implement efficient pheromone-based integrated pest management.

GC-EAD analyses of synthetic and weevil-produced phoenicol on a chiral Cyclodex-B-coated column (J&W Scientific) separated all four stereoisomers with base line resolution, and revealed the EAD-active stereoisomer (fig. 3) (Perez and others 1994). Lack of antennal response to non-weevil-produced stereoisomers indicated, and field

experiments confirmed, that non-natural isomers are not perceived and do not interfere with optimal attraction.

While electroantennograms (EAGs) require synthesis and electrophysiological assays of each optical isomer, GC-EAD analysis of stereoisomeric and weevil-produced phoenicol on a chiral column expeditiously disclosed activity of only the natural stereoisomer. Because non-natural isomers need to be perceived by the antenna to evoke behavioral inhibition, results indicated that stereosoimeric phoenicol was suitable for pheromone-based *R. phoenicis* management.

A GC-EAD system equipped with a chiral column should also facilitate and expedite chiral determination of novel scolytid aggregation pheromones with one, or like phoenicol, 2 chiral centers.

Conclusions

Many aggregation pheromones of scolytid and curculionid beetles have been identified (Borden 1985; Byers 1989), but critical semiochemical components for species already studied are yet to be discovered. Use of properly treated insects and suitable host trees as well as sophisticated technology (GC-EAD) will facilitate and/or expedite identification of novel semiochemicals which may improve semiochemical-based strategies and tactics against scolytid and curculionid beetles.

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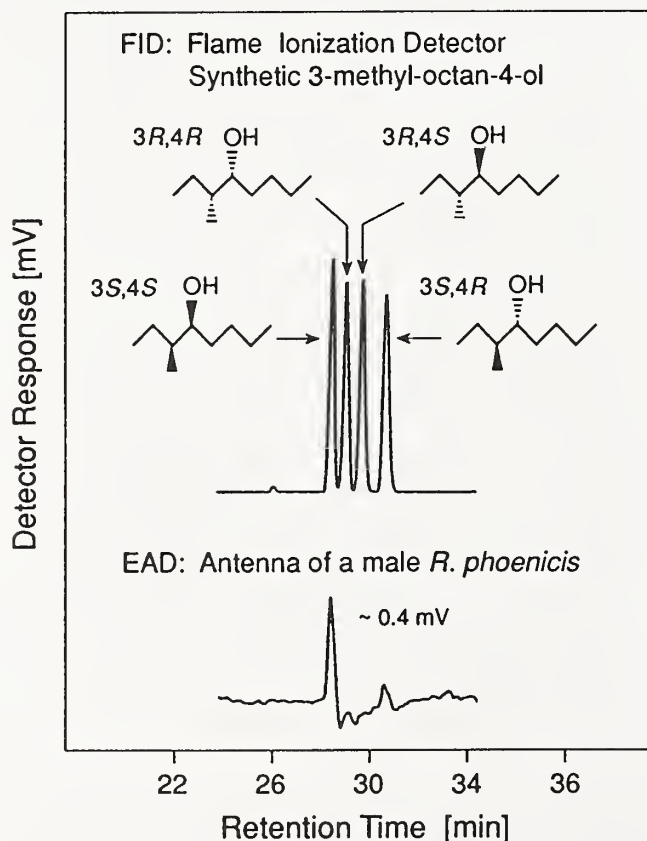
Figure 3—GC-EAD recording of a female *R. phoenicis* antenna responding to stereoisomers of 3-methyl-octan-4-ol chromatographed on a Cyclodex-B column (90 °C isothermal) (adapted from Perez and others 1994).

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Host Compounds as Semiochemicals for Bark Beetles

Kenneth R. Hobson

Abstract—In field tests, methyl chavicol is a strong anti-aggregant for several species of bark beetles. One low dose of methyl chavicol reduced aggregation by 40 to 68 percent for two species of *Dendroctonus* and two species of *Ips*. Methyl chavicol is a naturally occurring aromatic ether that is found in many species of hard pines. In ponderosa pine (*Pinus ponderosa* Laws.) and lodgepole pine (*P. contorta* Loud.) that were stressed by smog or disease and preferentially attacked by bark beetles, a 43 to 70 percent decrease in methyl chavicol was the largest phytochemical change compared to healthy control trees. Methyl chavicol may provide an olfactory chemical link to the observed ecological association of bark beetles with stressed trees. Study of the responses of bark beetles to host compounds with and without beetle pheromones holds great promise for integrating basic plant/herbivore research with applied efforts to develop semiochemical-based bark beetle management.

Host plant odors pervade the atmosphere in forests where bark beetles occur. The remarkable olfactory acuity of bark beetles to semiochemicals in their environment has been well demonstrated in pheromone research (Borden 1985; Wood 1982). However, our understanding of bark beetle responses to plant odors is in its infancy. Investigation of host plant odor and biochemistry with new biochemical analytical abilities should provide—and has already suggested—new semiochemical tools such as stereospecific attractants and interruptant kairomones. Such chemical tools can augment pheromone-based approaches to bark beetle management. Investigation of bark beetle response to host volatiles also provides a close link with basic plant/herbivore and plant stress studies. Recognizing the evolution of host and herbivore biotypes, and understanding the mechanism of herbivore selection of diseased or susceptible hosts are challenges we can address with detailed knowledge of the dynamics of plant secondary compounds and insect response to these changes.

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A Case Study: Methyl Chavicol

In the late 1960's a group at the University of California at Berkeley including R. W. Stark, D. L. Wood, J. R. Parmeter, Jr., F. W. Cobb, Jr., P. R. Miller, and others examined smog damaged trees that were being heavily attacked by western pine beetle (*Dendroctonus brevicomis* LeConte) and mountain pine beetle (*D. ponderosae* Hopkins) in the San Bernardino Mountains (Stark and others 1968). In papers that followed from that work, Cobb and others (1968, 1972) discussed methyl chavicol (= estragole), the second most abundant volatile of the foliage of healthy ponderosa pines (*Pinus ponderosa* Laws.). The 70 percent drop in methyl chavicol was by far the largest biochemical change detected in the damaged trees preferred by beetles.

More recently, T. E. Nebeker and others examined the biochemistry of lodgepole pine (*P. contorta* Loud.) diseased with comandra stem rust (*Cronartium comandrae* Pk.) or infected with armillaria root disease (*Armillaria* sp.). These are the trees in the Intermountain West most likely to be infested with mountain pine beetles (Amman and Schmitz 1988; Tkacz and Schmitz 1986). Nebeker and others (in preparation) found 43 and 62 percent reductions, respectively, in the level of methyl chavicol in these diseased trees. This was again the greatest biochemical change that occurred among the most abundant host compounds (all those present at greater than 0.1 percent).

Methyl chavicol or estragole is known by several other chemical synonyms including: allylanisole, isoanethole, p-allylmethoxybenzene, chavicol ether, esdragon, tarragon and 1-methoxy-4-2 (2-propenyl) benzene (Material Data Safety Sheet, Aldrich Chemical). It is a simple, licorice-smelling, aromatic ether or phenylpropanoid. Methyl chavicol is found in the xylem resin of many of the hard pines in the subgenus *Pinus* including ponderosa, lodgepole, loblolly (*P. taeda* L.), longleaf (*P. palustris* Mill), slash (*P. elliottii* Engelm.), Scots (*P. sylvestris* L.), black (*P. nigra* Arnold) (Mirov 1961), and Caribbean (*P. caribaea* Morelet) (Smith 1975). It is common in foliage of spruce, *Picea* spp. (E. Zavarin personal communication); and is distributed widely among other plant families. It also contributes to the flavors of several strongly scented herbs: fennel (*Foeniculum vulgare* Mill.), basil (*Ocimum basilicum* L.), clove (*Syzygium aromaticum* L. Merrill. L.M. Perry), tarragon (*Artemisisia dracunculus* L.), and star anise (*Illicium verum* Hook.f.) (Duke 1988). The most well known example of methyl chavicol as an insect kairomone is its role in the Cucurbitacae as an attractant of corn root worm beetles (*Diabrotica virgifera* LeConte) (Metcalf and Lampman 1989).

The responses of several bark beetle species to methyl chavicol have been observed in laboratory tests. In a variety of olfactometer tests, Werner (1972a,b) used host

extracts and pure host compounds alone and in combination with pheromones and found that methyl chavicol decreased the response of female and increased the response of male southern pine engravers (*Ips grandicollis* Eichoff). Payne and others isolated methyl chavicol from bolts infested with southern pine beetle (*Dendroctonus frontalis* Zimmermann) in the late 1970's. They tested southern pine beetle response to methyl chavicol in a walking bioassay and electroantennogram (EAG) (Payne, personal communication). In laboratory tests Gries and others (1988) identified methyl chavicol emanating from new galleries of the spruce beetle (*Dendroctonus rufipennis* Kirby); but no tests of its behavioral activity were conducted. In 1988 White measured the EAG response of the red turpentine beetle (*Dendroctonus valens* LeConte) to 11 of the most abundant volatiles from ponderosa pine resin (White and Hobson 1993). Methyl chavicol produced the third highest response for males and females. Whitehead, in preliminary work in 1993 tested mountain pine beetle's EAG response with methyl chavicol and found the fourth highest response of all host compounds tested (Whitehead personal communication).

At the 1992 national meeting of the Entomological Society of America, Hayes and others (1992) described the anti-aggregant effect of a "novel host compound" from southeastern pines that was strongly reduced in trees treated with metham-sodium and dimethyl sulfoxide. Treated trees were preferentially attacked by southern pine beetle after the level of this host compound was reduced. In field tests with Lindgren traps the repellency of the host compound compared well with verbenone. Hayes and others (in preparation) later reported on additional laboratory tests of this compound with several species of scolytids and revealed it to be 4-allylanisole (= methyl chavicol).

Metcalf and Lampman (1989) explored chemical variations of methyl chavicol with different simple side chains to discover the most potent attractant known for corn root worm—a "parakairomone" in their terms. In theory at least, one might test quite a large number of non-host compounds for interruption of attraction. Perhaps peppermint, wintergreen, or naphthalene moth balls would be super repellents. Hayes and others (in preparation) used several chemical analogues to methyl chavicol in laboratory repellency tests with southern pine beetle and found three that were at least as repellent as methyl chavicol.

Field tests of the response of five western bark beetles to methyl chavicol began in 1993. I tested western pine beetle, red turpentine beetle, and California fivespined ips (*Ips paraconfusus* Lanier) in California and mountain pine beetle and the pine engraver (*Ips pini* Say) in Idaho. Tests were designed to detect a positive or negative response to methyl chavicol with four treatments: (1) a blank control, (2) a sample of methyl chavicol, (3) an attractive pheromone or kairomone bait, and (4) the bait attractant plus methyl chavicol together. The test used a randomized block design with Lindgren traps. Treatments were randomly reassigned to traps after every collection of beetles. Methyl chavicol significantly reduced the catch of beetles with active bait by: 60 percent for western pine beetle, 68 percent for mountain pine beetle,

29 percent for pine engraver, and nonsignificantly by 21 percent for red turpentine beetle. In my preliminary work *I. paraconfusus* catch was reduced in five of six trials with too few replicates for a test. However, in additional preliminary work, Storer (1994) has since tested methyl chavicol on California fivespined ips at Berkeley using a similar experimental design and found an approximate 40 percent reduction in catch.

These results are preliminary; nevertheless the conclusion is clear. Methyl chavicol, a natural host compound, interrupts scolytid aggregation and decreases in concentration in the diseased or stressed trees that are most often attacked by aggressive bark beetles. This conclusion is exciting because it sets repellency by a host plant odor into the ecological context of what we already know about bark beetle association with diseased, stressed trees and it provides new possibilities for bark beetle management. There are of course caveats:

1. These data are from traps and not trees. Trees are notoriously difficult to protect from beetles.
2. Dose-response tests are needed to compare my release rate to natural emissions from healthy trees. But the release rate I used, approximately 0.5 ml/day is likely to be in the low range of what would be coming from healthy foliage.
3. This compound is in the foliage of ponderosa pine (and the cortical resin of lodgepole). Most bark beetle host selection work has considered volatiles from the xylem or cortical resin of the bole. However, there is something quite logical about beetles being influenced by foliage volatiles as that is where gas exchange takes place, where host volatile emissions mostly come from, and where biochemical changes are most pronounced with plant stress.
4. Deterrents/repellents/interruptants likely are only effective at short range, where an odor gradient from the tree exists. In contrast, attractants, even in broken up packets in moving air, can trigger anemotactic flight behavior that can draw insects to an attractive source 100's of meters away. A new mental model of how antiaggregants might work at distances greater than a few centimeters is needed.
5. Finally, this is probably not "the silver bullet" of host selection for these species. Trees are complicated sensory objects. Other host stimuli, including visual and olfactory cues, also play a role. To paraphrase Metcalf and Metcalf (1992): it is probable that no totally definable (host selection) message exists, since the chemical extent of the message is dependent on so many variables.

Nevertheless plant odor repellents do provide some interesting management possibilities. Pheromone repellents/interruptants such as verbenone have been plagued with still unexplained inconsistency (L. Rasmussen personal communication); and may, by themselves, be intrinsically unable to reliably protect trees because of their multifunctional nature, they also serve as attractants at low concentrations. Verbenone, produced by bark beetles, always signals the presence of bark beetles. This in itself may increase the probability that bark beetles will be drawn to the locality of the verbenone even if they are interrupted

from aggregating on the tree where verbenone is being released. In contrast, host antiaggregation compounds, such as methyl chavicol, signal only the presence of the (normally resistant) host and would not be likely to attract bark beetles at normal concentrations.

The reduction in trap catch with methyl chavicol for western pine beetle was of the same order of magnitude as that for verbenone. Methyl chavicol is one fifth as costly as verbenone ($77/kg versus $375/kg), much more abundant naturally, and readily available commercially. If the repellency of a plant odor is additive with the antiaggregation of verbenone, it may be possible by combination to come up with more dependable semiochemical protection.

Related Studies of Bark Beetles and Plant Volatiles

Recently other work has been published that shows antiaggregation by plant odors. Dickens and others (1992) showed that a combination of nonhost "green leaf volatiles" from broad-leaved plants significantly reduced the attraction of the southern pine engraver, the four spined engraver (*Ips avulsus* Eichoff), and southern pine beetle to their respective pheromones. Wilson (personal communication) in 1993 found significant reduction of attraction of female mountain pine beetle to green leaf volatiles. Similarly, Schroeder (1992) showed that the attraction of the European pine shoot beetle (*Tomicus piniperda* L.) and *Hylurgops palliatus* Gyll. to ethanol was interrupted or reduced by volatiles from wood of nonhost aspen (*Populus tremula* L.). *Trypodendron domesticum* L. and *Anisandrus dispar* F. are repelled by α-pinene from nonhosts Norway spruce (*Picea abies* L. Karst) and Scots pine (Nijholt and Schonherr 1976).

The somewhat random progress in elucidating bark beetle response to host odors is evidence of the need for basic research on a number of pertinent questions:

1. Which groups of compounds would most likely elicit a response from bark beetles? Are there classes of chemicals, such as aromatic ethers or alcohols, that most often are behaviorally active?
2. Is the probability of bark beetle response to a compound related to the frequency with which it is encountered? For example, are nonhost compounds more likely to produce antiaggregation when the non-host is frequently encountered by the beetle?
3. Several insect herbivores are attracted by allylisothiocyanate to their cruciferous hosts (Free and others 1978). Are unique or unusual, relatively host-specific compounds used by bark beetles to locate hosts or avoid nonhosts?
4. Are more general compounds such as the decomposition product ethanol often behaviorally active?
5. Do beetles respond to chemicals that increase or decrease strongly when trees are vigorous or are placed under stress?
6. Visser (1986) cited several examples of insect herbivores that are sensitive to the ratio of a blend of host odors. Is the ratio of several host compounds important in producing a response by bark beetles?

7. Are major host compounds such as α-pinene and β-pinene more or less likely to be behaviorally active than minor compounds?
8. Is the tendency of a compound to produce antiaggregation related to its toxicity to the beetle?

We also need to know about variability of bark beetle response to host odors. How does response vary regionally, seasonally, by sex, by dose or concentration, by beetle age and physiological state or by population phase (for example epidemic or endemic)?

Other basic questions that have practical importance include:

1. What other sensory stimuli, such as visual cues, combine synergistically with olfaction to increase bark beetle response?
2. Are different kairomones synergistic with each other?
3. Are kairomones additive or synergistic with various pheromones?
4. How far away from a source can plant odors cause beetle avoidance or attraction?
5. When in the host selection process do plant compounds have their effect, prior to landing or later after feeding?

Many of these questions have been addressed in the study of bark beetle pheromones and methods exist to answer them. Others are being explored in studies of other herbivores. Insights from these studies should be incorporated in our study of bark beetles. When we better understand the role of host odors in scolytid chemical ecology, we will be able to better implement practical semiochemical-based management of bark beetles.

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Technology Transfer: Crossing the Barrier from Research to Operational Use of Tactics by Nonentomologists

James E. Johnson

Abstract—Technology transfer is a vital part of the adoption of new products or processes. In forestry, technology transfer activities are usually conducted by the U.S. Department of Agriculture, Cooperative Extension Service, the Forest Service, State and Private Forestry branch, or State agencies. Elements of successful technology transfer programs involve appropriate audience identification, needs and current knowledge assessment, program delivery, and evaluation. Future emphasis on accountability will favor developmental programming, with evaluation of KASA (knowledge, attitudes, skills, and aspirations) and practice changes, and end results.

Technology transfer is simply the process of conveying new information in a form that can be understood and evaluated, and which will result in an informed decision to reject or adopt an approach, idea, or innovation (Hobbs and others 1993). The technology may or may not be a new invention or approach, but may simply be an established practice or concept that is new to the audience. Since the entering of people into a field is a very dynamic process, there is a continual need for technology transfer to new audiences, even if the technology is well established.

In reality, technology transfer programs in forestry are often not put into place until well after the technology is developed and tested. This is beneficial in that the technology is fairly well-proven by the time it goes to the field. The down side, however, is that there is a long lag period before practices become operational and most commonly the technology transfer specialists are not involved in the research phase. In an ideal world, the plan for transferring the technology would become a part of the research plan from the beginning, so that an Extension specialist would have input and receive the necessary funding to effect a truly desirable outcome. There are examples in forestry where this approach has been successfully implemented, including the Forestry Intensified Research (FIR) program in Oregon and the integrated science and management program at the University of British Columbia (Namkoong 1993).

There are a number of organizations, agencies, and models for technology transfer programs operating in forestry in the U.S. Perhaps the most widely known is the U.S. Department of Agriculture, Cooperative Extension Service, which operates through subject matter specialists at land-grant universities, local areas, or counties. Extension personnel transfer technology developed at their own universities, as well as others. The success of Extension programs often depends on a strong partnership with the researcher and with other Extension personnel. The U.S. Department of Agriculture, Forest Service, State and Private Forestry arm is especially active in technology transfer within the area of forest pest management. The degree of cooperation between the Forest Service and Extension Service varies around the country, with outstanding relationships existing in some areas, and turf problems existing in others. Many university-industry cooperatives exist, with technology transfer an active part of the cooperative. Also, many State forestry agencies have assumed an information and education role, particularly with private landowners.

Successful Technology Transfer Program

Audience Identification

The first key event in a successful technology transfer program is to determine who the target audience is. Once the audience is defined, certain important characteristics that will impact program delivery can be ascertained. For example, is the audience defined as a professional group, such as State agency personnel, industrial foresters, and consultants, or is the target audience really the private landowner? If a professional audience is defined, how can that audience best be reached? What is its sensitivity to time, cost, and location of technology transfer programs? It is possible to develop an outstanding program that ultimately fails simply because the program was scheduled for the wrong time of year; for example, during planting or fire season. If the technology transfer needs are general, covering a wide audience of both professionals and non-professionals, it may be necessary to develop separate programs.

Assessment of Audience Knowledge

A simple, but often overlooked, component of a technology transfer program is an assessment of the current level of knowledge of the audience. This is important because

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it provides a yardstick against which to measure the success of the program. For example, if the target audience for a program on using semiochemicals to slow the spread of southern pine bark beetles is defined as State agency foresters, it would be prudent to develop some instrument to assess their current level of knowledge. Do the foresters know how to identify different species of beetles? Can they determine the stage of infestation or the direction of spread? Can they provide adequate silvicultural recommendations? If their current level of knowledge is known, the program can be more effectively evaluated.

Design of a Delivery System

Once the audience has been identified and assessed, planning for an appropriate delivery system can begin (Garland and Adams 1992). There are many tools available today for delivering information. Traditional avenues such as Extension bulletins and field days, tours, and seminars, are tried and true, and still continue to be the mainstay of many technology transfer specialists. Videotapes and video teleconferencing (Anderson 1993) are becoming more popular, as are electronic bulletin boards and server groups on Internet. Electronic devices for the storage and retrieval of technology transfer information are also becoming more popular. Examples include CD-ROM and university-based systems such as Penn Pages, developed by Penn State University, and GOPHER, developed by the University of Minnesota.

Despite all the excitement that these electronic innovations provide, the fact remains that professional foresters tend to be a traditional group. They would rather go to the field to view first-hand a new practice or innovation than watch it on television. First-person programs, commonly with an associated field trip, will continue to be the most effective way to influence this audience.

It is important to point out that no one delivery system will always work the best. A combination of traditional printed materials, a videotape, and a 2-day workshop with field trip may be the best system for a given audience and technology. This program may refer the participants to an electronic bulletin board for more current updates.

An example of the interaction between the generation and adoption of a new technology is displayed in figure 1. In this example, the technology transfer agency is the Cooperative Extension Service. Research agencies or industry develop the technology, adapt it for commercial use in cooperation with others, and provide the marketing and financial assistance. The Cooperative Extension Service is involved in the education and technology transfer activities (stage 3 in figure 1). In the future, much technology transfer will be done by consortia or cooperative agreements between the public and private sector (Bennett 1992, 1993).

Program Evaluation

Technology transfer programs can be classified as "informational" or "developmental." Informational programs are provided simply to inform an audience, with no further expectations. For example, a generalized Extension bulletin on the life history of the southern pine beetle is an

example of an informational item. The major objective of this low level type of programming is to increase the awareness of the audience, to make participants better informed about a particular issue, product, or approach. On the other hand, developmental programming involves the movement of an audience from some preliminary level of knowledge or activity to a measurable, higher level. Inherent in developmental programming is the need to carefully evaluate the program, often many months or years afterward.

The Cooperative Extension Service has identified a series of seven levels of Extension programming, as follows:

Level	Activity
1	Inputs
2	Activities
3	People involvement
4	Reactions
5	KASA change
6	Practice change
7	End result

Most commonly, programs are evaluated at level 4, which would include immediate postprogram surveys. Developmental programming should, however, be evaluated at levels 5 through 7. KASA changes refer to knowledge,
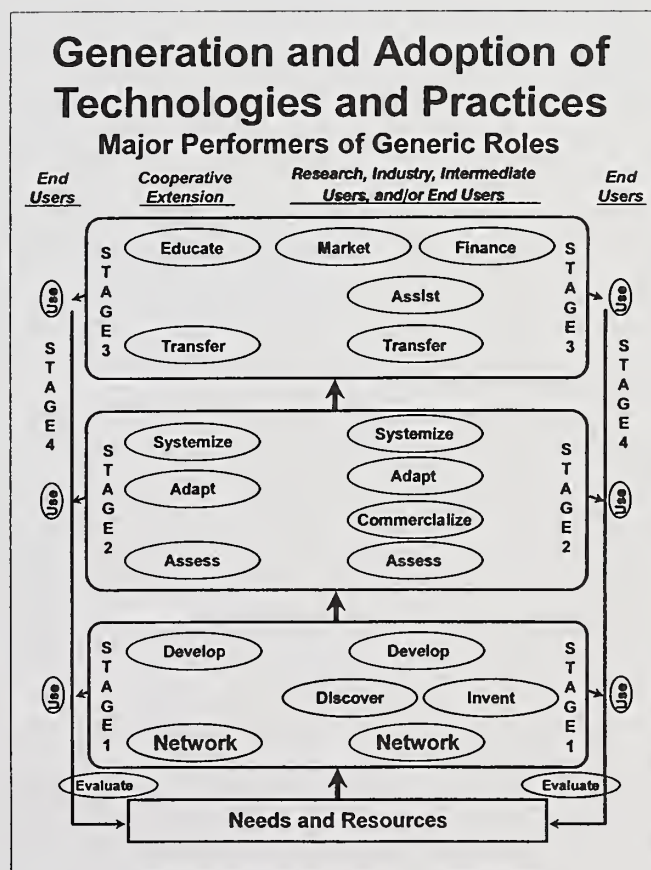

Figure 1—Interdependence model of generic roles performed within the public/private sector complex (USDA, CES 1992).

attitudes, skills, and aspirations. A specific program should be targeted at these audience attributes. Evaluation some reasonable time after the program should be targeted at level 6, or the practice change. Changes in practices will ultimately lead to level 7, or the end result of the program. Often, the results will be long term in nature, and easily identified at any point in time. Given the example of introducing the new technology of semiochemical control of bark beetles, what can be expected in terms of KASA changes? The target audience, agency foresters, can learn how the control strategies can be more effective than current control measures, can become turned on to this new technology and become proficient at recognizing where and how it can be used to protect the woodlands they manage. This may result in a practice change so that these products become the standard means of control in certain instances. The number of hectares upon which this control strategy has been implemented over the 5-year period following the technology transfer program provides a measure of the end result.

Conclusions

Technology transfer programs are more important today than ever before. As new products, approaches, and issues surface, teams of Extension specialists and information/education personnel will be called in to conduct a myriad of programs. Although the technology of program delivery has also dramatically increased in recent years, traditional programs for traditional forestry audiences will continue to be the most effective tools. However, there is a new emphasis on accountability, and new and improved evaluation procedures will need to be implemented in many cases. If technology transfer specialists expect a slice of the research dollars to conduct their activities, they will have to spend time on proper program evaluation.

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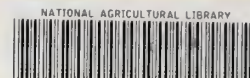
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